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# *ANALYSIS OF VARIANCE APPLIED TO HUMAN GENETICS*

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Analysis of Variance is a well-known convenient mathematical device by which the total of all squared deviations from the grand mean of some heterogeneous population may be divided into 2 variances, namely, variability about the mean of each of the more homogeneous elements in that population and the variability of these partial means about the grand mean of the entire population. It can be used to answer the question, how does the variability within the homogeneous or elementary group compare with the variability of the groups between one another? For example, how does the variability of the fruits of any one tree of a species compare with the variability of the average fruits of different trees of that species?

So far as I know the technique of Analysis of Variance has not yet been applied to human traits measured in a number of fraternities in a population. An opportunity came to me to make this application in the variance of some 14 head measurements made on the boys of 6 families, containing each from 5 to 3 boys. These dimensions were taken at age 16 years exactly or, in a few cases, by interpolation or extrapolation of a year.

The details of handling these sets of variables are well known and need not be considered here. The results are given in the accompanying table. The $F$ values are the quotient of the larger mean square by the smaller mean square. The size of the quotient determines the chances that the $F$ values are due merely to sampling and accordingly fail to indicate a significant difference between the two sorts of variances—within fraternities and between fraternities.

The table reveals that the mean squared variance within a family is, in all 13 traits, *less* than the variance between families, and that the ratio of one to the other is always significant and usually highly significant.

To go into some detail one may point out that the mean square variance in respect to *face width* between 16-year-old boys of one fraternity is one-twelfth that between different families even when all these families are of

"Old American" stock and when the boys in the different fraternities are being reared under practically identical conditions in an institution so that differences due to environment merely are minimal. Hence *face width*, or bizygomatic width, is determined very strongly by common intrafamilial genetical factors, while between families there are fewer common genetical factors.

In the *interpupillary distance*, similarly, the variance inside a fraternity is one-tenth that between fraternities. If one examines the entire table it appears that the lateral head dimensions—bizygomatic width, interpupillary distance, forehead width, maximum head width, distance between inner eye angles—have large $F$ values while vertical dimensions such as elements of facil height have smaller $F$ values. Bigonial diameter and nasion to gnathion are somewhat out of order with this general rule.

Thus it appears that the ratio of variability inside fraternities to that between fraternities is greater in lateral dimensions than in vertical dimensions; just why cannot now be said.

The Analysis of Variance illustrates the obvious fact of difference in variation (both intra- and interfraternal) according to the degree of heterogeneity of the gene complex. In monozygotic twins, between whom the genes are apparently the same, heredity influences the end result by 95 per cent or more. In general, between members of the same fraternity, more or less of the genes are unlike depending upon the greater or less remoteness of the stocks of the two parents. Where the parents are cousins variance in the fraternity is low. Where the parents are heterozygotes of two human races (as in negro-white crosses) the variances of the nasal dimensions and skin color are high.

*Between mean of fraternities* of the *same stable community*, more or less homogeneous in racial stock, variance will be relatively low. As the community becomes more heterogeneous mean variance between fraternities will increase and likewise the value of $F$. As an extreme case we can imagine a breeder of dogs, cats, guinea pigs and rabbits, who had a large litter of each species and compared variance in ear length within fraternities and between fraternities without separating species. In this example there are still fewer traits in common between the ear lengths of the species so that variance between the fraternities (and $F$) would be very large. In general, if few genes are involved in building any organ interfamilial variance will not be strikingly greater than intrafamilial variance. If many genes are involved then the cluster found in one fraternity may well differ markedly from that found in another fraternity, so that interfraternal variance, and $F$, will be relatively large.

By the application of the method of Analysis of Variance we may in time gain some notion of relative number of genes involved in the development of an organ—or, in other words, its genetic complexity

ANALYSIS OF VARIANCE OF HUMAN HEAD MEASUREMENTS

| TRAIT | MEAN SQUARE VARIANCE BETWEEN FAMILIES | MEAN SQUARE VARIANCE WITHIN A FAMILY | $F$ VALUES |
|---|---|---|---|
| Chances under 1 per 100 that $F$ values are due to sampling | | | |
| Bizygomatic width | 155.02 | 12.50 | 12.40 |
| Interpupillary dist. | 42.71 | 4.38 | 9.85 |
| Minimum frontal width | 123.77 | 14.54 | 8.51 |
| Head width | 98.63 | 13.41 | 7.36 |
| Head girth | 711.30 | 107.42 | 6.62 |
| Dist. bet. inner eye ang. | 17.47 | 2.78 | 6.29 |
| Trichion to gnathion | 254.19 | 46.59 | 5.46 |
| Nasion to gnathion | 129.45 | 24.80 | 5.22 |
| Head length | 80.94 | 16.95 | 4.78 |
| Head height | 54.44 | 12.62 | 4.32 |
| Chances 1 to 5 per 100 that $F$ values are due to sampling | | | |
| Bigonial diameter | 70.44 | 18.23 | 3.87 |
| Nasion to stomion | 43.38 | 14.66 | 2.96 |
| Chances over 5 per 100 that $F$ values are due to sampling | | | |
| Trichion to nasion | 47.77 | 18.01 | 2.65 |
| Stomion to gnathion | 31.55 | 13.14 | 2.40 |

## *TWO X-RAY INDUCED MOSAICS IN DROSOPHILA PSEUDOÖBSCURA*

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The mechanism of the origin of chromosomal aberrations is still an open question. The so-called contact hypothesis, advanced originally by Serebrovsky,[1] assumes that translocations and other gene rearrangements are formed due to chance union of chromosomes accompanied by the development of new associations between genes, somewhat in the manner of "illegitimate" crossing-over. According to this view, the breakage of the original chromosomes and the reattachment of the resulting fragments occur practically simultaneously. The alternative hypothesis assumes that chromosomes are broken first, and that some time may elapse before the points of fracture either reunite to restore the original situation or form new attachments.[2,3] Unfortunately, the problem is such that critical evidence has been difficult to obtain.[4, 5, 6, 7] The mosaic translocations described below may possibly shed some light on the question.

Normal males of race *A* of *Drosophila pseudoöbscura* were treated with x-ray (5000) units, and outcrossed to normal untreated females. The

salivary glands of the $F_1$ larvae were taken, stained in aceto-carmine, and permanent smear preparations were made with the aid of the usual technique. Each slide contained only the two glands of a single individual. In the course of study of these slides, two very remarkable aberrant sets of glands were found. Instead of having the customary single type of tissue, either completely normal or having all cells containing the same aberration, these two sets of glands were mosaics of more than one kind of tissue. Several facts show that this result cannot be due to contamination (i.e., mixing the glands of several individuals in the same slide). In the first place each slide contains two and only two glands; in these particular slides the two glands lie separately. Secondly, both glands of each set are of the same sex. Thirdly, and this is the main argument, both glands of each set contain mixtures of tissues, the same cytological condition being observed in some cells of either gland.

The more complex of the two sets of mosaic glands apparently contains four different tissues. An analysis was made of each of the glands of this mosaic. In one gland, a total of 42 cells proved to be satisfactorily analyzable; the precise status of 8 cells was in doubt and the rest were not clear enough to attempt a classification. The four types of cells are as follows. The first, and by far the most frequent type, observed in 58% (24 out of 42) cells examined, departs from normal in having a translocation between the third and probably the *Y*-chromosomes (Fig. 1*a*). In terms of the maps published by Dobzhansky and Tan,[8] the third chromosome is broken in section 80, between the first and the second dark discs distal to the "bulb." As the *Y*-chromosome in salivary glands is not a distinct body, being simply a part of the heterochromatic chromocenter, it is impossible to determine the position of the break in this chromosome. The second type of cells (11% of the total analyzed) contains a translocation involving the third and the fourth chromosomes (Fig. 1*b*). The third is broken at about the middle of section 66, and the fourth is broken in section 97, the major part of the third being exchanged for the distal end of the fourth chromosome. The third type of cell (19%) is a combination of the preceding two, i.e., the III–*Y* translocation is present together with the III–IV one (Fig. 1*c*). Finally, the fourth type (11%) are normal cells, apparently free from any cytologically detectable abnormality. The second gland of this set contained 15 analyzable cells, 12 doubtful ones and the rest too poor for classification. Again the most frequent type of cell was that having the III–*Y* translocation (11 out of 15). There was only one clear-cut example of the III–IV translocation, none of the III–*Y*, III–IV; and three examples of normal third chromosomes.

Several mechanisms which may produce such a mosaic may be suggested. If one were to suppose that two sperm fertilized a single egg and that each one had one chromosome aberration in it, a mosaic individual

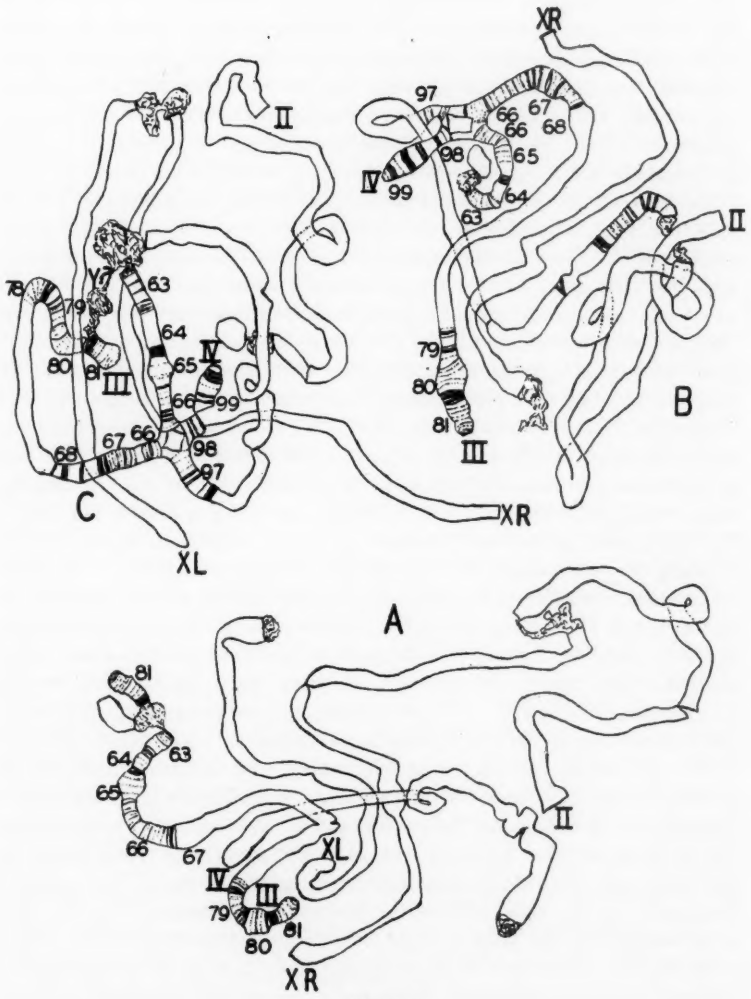


FIGURE 1

Three types of aberrant tissue found in the salivary glands of an $F_1$ male offspring from a cross between x-rayed males to normal females. *A*—translocation involving the tip of III and the *Y*-chromosome, *B*—translocation between the base of III and the tip of IV, *C*—combination of translocations *A* and *B*.

would result. Such an individual might have two different types of salivary gland tissue. That it is possible for both nuclei of the first cleavage division to be incorporated in the salivary gland tissue is supported by recent work of Kaufmann.[9] The points in the present evidence which automatically rule out this hypothesis are that not two but four types of tissues are present, and that one of these contains an aberration combining the properties of the two other aberrant types (Figs. 1*a* and 1*b*). Another possibility is that x-rays as such had no effect on the sperm, but that during the course of the development three types of the aberrant tissues arose spontaneously. A spontaneous translocation has been described in an individual of *Drosophila melanogaster* that has not been treated with x-ray, and this individual has been a mosaic of normal and aberrant tissue.[10] Since spontaneous chromosomal changes are relatively very rare, to suppose that so rare an event takes place three times in the development of a single individual is, however, too improbable. Still another possibility is that one translocation took place due to the irradiation (for example the III–*Y* translocation), and then another (the III–IV translocation) occurred spontaneously after fertilization in a part of the modified tissue. This view is also ruled out because of two securely established facts, namely the presence of cells with the III–IV but without the III–*Y* translocation, and of the apparently normal cells containing neither translocation. A somatic crossing-over would have to be invoked to produce these additional types.

The fourth possibility is one which assumes that the chromosomes in the sperm are in the four-strand stage. Were such the case a workable hypothesis could be developed to account for the formation of a four-tissue mosaic. For example, if one supposed that the breaks induced by the x-ray at any level effect only two of the four strands present, and if in the third chromosome two of the strands are broken in region 80, whereas the other two are broken in region 66, a cross-over occurring between one strand broken at 80 and one broken at 66 would result in one unbroken normal strand, one broken both at 80 and at 66, one broken at 80 and the fourth broken at 66. Reattachment of broken parts might occur before the chromosomes went into the first cleavage spindle. Then, all these suppositions granted, the segregation in the first and the second cleavages must be such that each of the resulting four nuclei contains one of the four types of cells found. The main weakness of this hypothesis is the assumption of crossing-over among the four strands of a chromosome of a haploid group.

The fifth possibility, and the one which seems most probable to the author on the basis of the available evidence, is that the breakage of the chromosomes due to x-rays need not occur at the time of the treatment but may be delayed for one or more cell generations. Let it be assumed that the action of the x-rays has weakened, or actually broken, the third chromosome in two places, in sections 80 and in 66, the fourth chromosome in sec-

tion 97 and the *Y*-chromosome at an undetermined point. Such a sperm has fertilized a normal egg. During the process of the chromosome splitting in the first two cleavage divisions the weaknesses or the breaks in the chromosomes have persisted. In one of the resulting cells the broken ends have become reunited to restore the original gene arrangements, thus giving rise to cells with normal chromosomes. In one of these normal cells, before the weaknesses have become healed, an exchange has occurred between the third chromosome and the *Y*-chromosome. This would give rise to the III–*Y* aberration. In another cell, or cells, an exchange has taken place between the fragments of the third and the fourth chromosomes which is later followed by an exchange between the third and the *Y*-chromosomes. Thus the four types of tissue have arisen containing a III–IV translocation, a III–*Y* translocation and a combination of the two.

The rather involved character of the above explanation must be admitted, but it seems to be the one that best fits the observed facts. It must be noted, however, that it is not entirely unprecedented. Indeed, Lewitsky and Araratian[11] have described a mosaic translocation in a root of a Crepis seed treated with x-ray, in which some cells were normal, others contained a translocation involving certain chromosomes and still others had the chromosomes further modified, with the first modification being preserved. Lewitsky and Araratian's observations, as well as the facts presented in this article, constitute evidence in favor of the view that breakage, or "weakening" of the chromosomes due to irradiation with x-rays precedes the reattachment and formation of aberrations.

The second mosaic pair of salivary glands contained only two types of tissue. The aberrant tissue consisted of an inversion in the second chromosome from the proximal part of region 43 to the distal part of region 45. The other type of tissue was normal. In one of the two glands 32 out of 48 analyzable cells contained the aberration, in the other gland, out of 36 analyzable cells, 15 were aberrant. This mosaic is not critical as an evidence for the "breakage first" hypothesis, since any one of several mechanisms might have produced it.

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# THE SIZE OF THE TOBACCO MOSAIC PARTICLE FROM X-RAY DETERMINATIONS*

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The size of the tobacco mosaic particle has been determined by two techniques, filtration through pores of calculated dimensions and rate of fall in a field of known force. These size determinations lead to quite different results, the filtration size being larger than that estimated from the ultra centrifuge. Both methods are subject to technical difficulties and mathematical assumptions which, if not fully met, may lead to erroneous conclusions. But there are, as critical thinkers point out, even greater intrinsic difficulties with these techniques. If the ultimate virus particle is a rather small molecule which is adsorbed to a larger inert complex, both techniques will err on the side of assigning too large a size to the disease-producing particle. A quite different technique is needed to substantiate the estimated size measurement. This technique may be available in x-ray studies of the virus.

X-rays, like light, mark out the size of an object as the blacked-out area in which they are absorbed. In visible light this area is delimited on an optical micrometer. With x-rays the area may be found from the inactivation produced in the absorbing medium. The x-ray size estimate, in contradistinction to estimates based on filtration or ultra-centrifuging, is dependent on the size of the ultimate entity inactivated, not on any inert material to which it may be adsorbed. If the virus particle of tobacco mosaic is minute the rate of inactivation should be very moderate. If larger the inactivation rate should be more rapid. These rates are independent of any materials to which the virus particle might be adsorbed. The difference in rates would be present whether the true virus was free to move or fixed to inert matter.

Ordinary tobacco mosaic and several of its derivatives have been irradiated with x-rays from three metals, chromium, copper and silver. The effective wave-lengths from these tubes were 2.1, 1.5 and 0.7 Angströms.

Figure 1 shows certain of the survival curves obtained by treating tobacco mosaic and its derivatives with x-rays.

The inactivation rates of ordinary mosaic and the derivatives are essentially alike. They are concordant in showing a wave-length effect. The type of effect exhibited is explicable on the hypothesis that one absorption of x-ray energy within that portion of the particle is sufficient to inactivate it. The average size of this vital volume of the mosaic particle determined from these different wave-lengths is $7.5 \times 10^{-18}$ cm.[3] The data on organic

crystals show that the interatomic distances between atoms vary between 1 and 3$A$ with 2$A$ as a fair average. With an atomic spacing of 2$A$ this volume, which in our material has to do with reproduction, is equivalent to about 940,000 atoms. Seemingly highly purified materials, carrying the properties of tobacco mosaic are made up by percentage composition of 51.0 C, 7.1 H, 16.7 N, 0.5 S, 0.5 P and 2.5 carbohydrates.[1] The average atomic weight of this material is 16, or it corresponds rather well with that of most proteins. Multiplying the atomic volume of the portion having to do with reproduction by this value gives 15,000,000 as the molecular weight of this volume.

The estimated minimum molecular weight of the whole molecule by Svedberg[2] from ultra-centrifugal analysis is 17,000,000. The reproductive

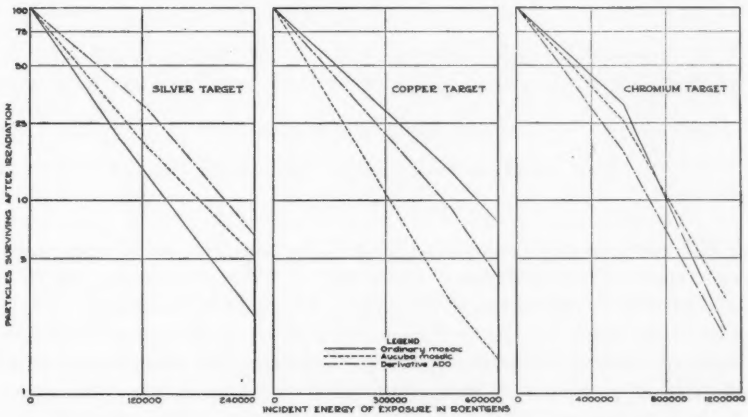


FIGURE 1

Survival curves of 3 tobacco mosaic viruses when exposed to roentgen rays of 3 wave lengths.

volume as determined above is less than this total volume but not very much less, a result which seems reasonable in view of the importance of reproduction in the organized world. The span between 15 and 17 million is left for atomic rearrangements which are not lethal to the organism. This span is known to be partly filled in as the mosaic diseases may mutate to other forms which retain the original reproductive capacity. We should expect this rate of mutation under x-rays to be quite small, an expectation which checks with our experience. Other approaches to the problem indicate that the virus entity is in the nature of a repeat molecule and may have a molecular weight of 40 to 100 million, a conclusion which gives added significance to the relative strengths of the bonds between the different molecular elements.

The data from our x-ray experiments are in agreement in viewing the tobacco mosaic virus as a rather large molecule of 16 to 20 million in molecular weight. The large portion of this molecule is important to its reproduction leaving a smaller portion capable of change without effecting this power to reproduce.

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## *"PERSONALITY" DIFFERENCES AS DESCRIBED BY INVARIANT PROPERTIES OF INDIVIDUALS IN INTERACTION*

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For many years, workers in social and psychological subjects have been concerned with the problem of "personality." This term is taken to mean a particular organization of behavioral elements, characteristic of the individual, which are supposed to be the product of the action of heredity and environment. Unfortunately, the discussion has been based almost entirely upon subjective impressions, and hence not only are we unable to define the properties of this entity in a precise and quantitative fashion, but also we cannot do more than hazard guesses as to the forces producing it. Attempts to define "personality" have either been in terms of a qualitative isolation of traits regarded as constituents of this entity,[1] or else they have been devoted, again qualitatively, to the task of describing and classifying individuals into "types."[2] From our own experience, we recognize that individuals differ from one another in what we call their "character" and "temperament," and we feel intuitively that this is of importance in determining how they get on with other individuals; but up to the present time, no quantitative definition has been attempted.

In a previous communication,[3] some preliminary results of the measurement of human interaction were presented, and it was there indicated that there are definite uniformities in the interaction of individuals. The facts described, however, were obtained by the use of a very crude measuring device which did not adequately describe the phenomena (durations of actions and inactions with two individuals). The present paper is a

report on some results obtained with an instrument with which this adequacy can be approximated. The results to be presented bear upon the problem of "personality," and a few words may help fix in the mind of the reader the significance of the procedures used.

The methods of the exact sciences are based upon the premise that relationships of functional dependence can be defined in the phenomena investigated. In order to isolate these relationships, units of measurement are defined, and the quantitative treatment consists in formulating relationships of functional dependence in terms of measured values of the variables.[4] If we are to use these methods, the problem of the "personality," as something apart from the influences operating on the individual, may be stated as the problem of demonstrating invariant properties of the behavior of the individual when subjected to these influences. Such individual differences have been demonstrated in a number of physiological investigations of the relationship of measured features of the performance of an organism and values of such known controlling variables as intensity of light and area on the retina,[5] fixed flash frequencies and intensity of light,[6] and so on. These differences would probably not be regarded as properties of the "personality," since "personality" is often considered to be exhibited in the relations of an individual with other individuals. If we are to demonstrate such invariant properties of the individual, they must then be isolated when that individual's performance is associated with the performance of one or more other individuals. From an operational point of view we are restricted to the observation of the interaction of individuals.[7]

In order to secure more accurate measurements of interaction, a recording device was constructed,[8] consisting essentially of a moving tape traveling at a speed of five inches *per* minute on which continuous lines are drawn by revolving, self-inking wheels. Each wheel is attached to a lever and activated independently when its key is pressed by the observer. When one individual acts, the observer presses the key assigned to that person, and the wheel lifts off the paper, not returning until the individual stops acting, when the key is released. To secure a measure of the alternation of action and inaction, one has only to measure with a scale (in seconds) the length of each inked line (inaction), and each empty space (action). By reading across from the line of one individual ($A$) to that of another ($B$), we can also obtain measures of the length of time that $A$ acts and $B$ is silent; when both $A$ and $B$ are acting (double actions); when both $A$ and $B$ are inactive or silent (double silence), and when individual $B$ acts and $A$ is silent.

The records discussed in this paper include over fifty conversations between the members of pairs of individuals, each observation lasting between thirty-five and forty-five minutes. These individuals talked in

a room, separated from the observer by a one-way screen. There were twelve individuals, not all of whom interacted with each other. Eight persons are dealt with here; the series of the other four being too short.

When frequency distributions were made of the durations of actions of an individual and again for his silences, it was seen that for both actions and silences the distributions were markedly J-shaped. To rectify the curve of the frequency, log $F$ was plotted as a function of $t$ and in some instances a good fit was obtained. In the majority of cases, however, there appeared to be a definite tail to the distribution; that is, in the longer durations there was a greater observed frequency than expected. When the residuals were plotted against $t$ it was found that this distribution was also J-shaped and a plot of log $F$ against $t$ again approximated a straight line. Accordingly it was judged that the function could be fitted by the expression[9]

$$F = ae^{-bt} + ce^{-dt}. \qquad (1)$$

For the eight individuals considered, eighty-two action and eighty-two silence distributions were plotted and the constants calculated.[10] In this paper we shall be concerned only with the constants $b$ and $d$ which define the slopes of the function. The constants $a$ and $c$, which define the height of the curve in respect to the ordinate, will not be considered here.

It must be understood that a steep slope, say for actions, indicates that there are many more actions of short duration relative to the longer intervals than there are in a flat slope. For our purposes, a steep slope might have a constant whose value was $-0.300$ or higher, while a flat slope might have a constant under $-0.100$. Therefore, as the long durations become exponentially more frequent relative to the short ones, the value of the constant decreases; conversely, as the short actions become more frequent, the value of the constant rises.

We have now to consider whether there is any functional dependence between the $b$ and $d$ slopes which we ordinarily obtain for both actions and silences, remembering that the $b$ slope describes the exponential distribution of the shorter values, beginning with those under 1 second, and the $d$ slope describes the frequency distribution of values running well up (in many cases) over twenty seconds—in other words, where an individual is either very silent or very talkative.

From observation, we know that individuals ordinarily exhibit a rough dependence between the durations of actions and silences; when a person becomes very talkative, for example, his silences become much shorter in duration. Since the $b$ slopes on the one hand measure the relative distribution of long and short values within the shorter durations observed, while the $d$ slopes measure a similar distribution in the long values, we should expect that there might be some sort of dependence between the

$b$ and $d$ slopes. If $b_a/b_s$ is plotted as a function of $d_a/d_s$, it is found that log $b$ ratio is a rectilinear declining function of log $d$ ratio, with a slope of 1.

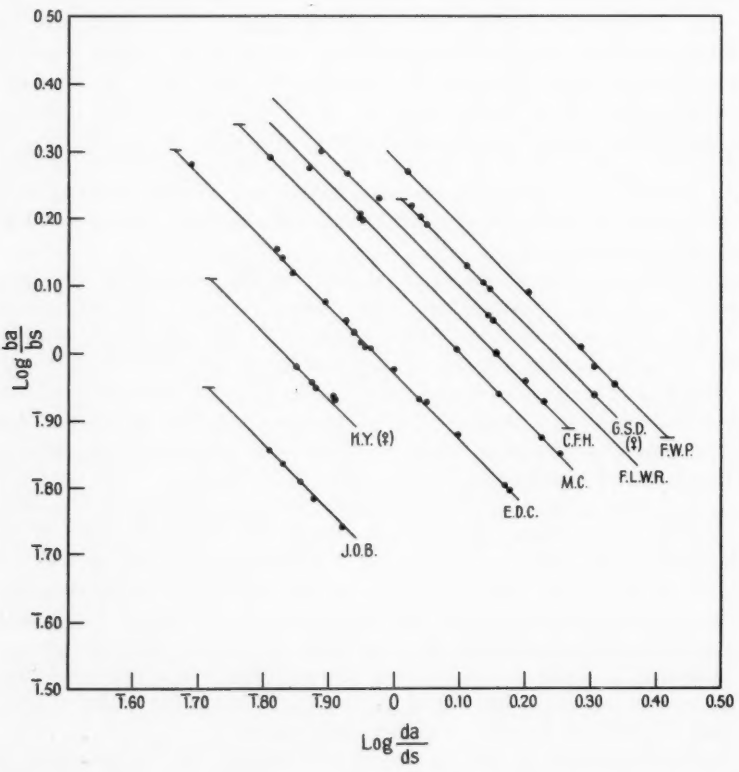
$$\log b_a/b_s = -\log d_a/d_s. \qquad (2)$$

When all the cases in which an individual manifests two $d$ slopes are plotted, it is found that all his points fall on the line defined by the above equation (2), no matter with whom he or she was interacting. In figure 1, which gives the data of eight individuals, each individual has his own curve, although the slopes ($=1$) are all the same. This means that the actual rate of adjustment of the $b$ ratio in respect to the $d$ ratio is *unique* for each individual, although the *relative* rate is the same. In the eight curves presented, with the exception of *FLWR*, each person interacts with at least two persons, and *EDC*, the longest series, interacts with five different people. Since the position of the line does not shift in the data for different pairs including the same individual, we may consider that the position of the curve (defined by the ordinate intercept) is *invariant* for the individual.

There is additional evidence that not only the position of the curve but also its length (span) may tend to be invariant for the individual. In a small number of cases in each series, no $d$ curve was found either in the silences or in the actions. If the position of this observation be calculated from the $b$ ratio, it was found that in all cases in which no $d$ slope is found (where $N$ is large enough to expect one to occur), the value of the $b$ ratio is either greater or less than any value in which a $d$ ratio appears. Moreover, the absence of a $d$ slope occurs systematically. When the value of the $b$ ratio is less than the lowest value recorded with the $d$ ratio, then uniformly no $d$ silence slope appears; conversely, when the value of the $b$ ratio is greater than any in which both $d$ slopes appear, then no $d$ action slope appears. Not only then is the position of the curve of this function (2) invariant on a double log grid, but also the limits within which both $d$ slopes appear also seems to be invariant for the individual on the present evidence. In figure 1, the limits of the appearance of $d$ ratios are fixed by lines drawn across the line of the individual at the first value of the $b$ ratio in which no $d$ action or silence slope appears.

The significance of this functional relationship may become clear if we regard the individual as interacting in three "states" as defined by this function. In the first, where there is no $d$ silence curve, the value of the $b$ ratio is below the limits defined by log $b$ ratio equals minus log $d$ ratio. This means that the $b$ action slope is so flat and the $b$ silence slope so steep that the individual has reached a kind of limit in talkativeness such that he does not manifest any long silences. In the other limiting case, where there is no $d$ action slope, the value of the silences in the $b$ slope is so low that there is no variation from a uniform rate of long silences. No long

actions sufficient to produce a *d* slope appear. In both these cases, however, the individual varies in his action or silent rate, that is, there is both a *b* and a *d* curve for actions if *d* silence is missing, and vice versa. In the intermediate state, there is dependence between four slopes, such that if the *b* action slope increases (more short actions appearing) and the *b* silence remains constant or becomes flatter, then the *d* action slope becomes flatter (contains relatively more long actions) or the *d* silence curve




becomes steeper. In other words, as a man becomes talkative he talks in longer durations, and there is a decline in the frequency of long durations and an increase in the short in the *b* action slope which describes the shorter actions, or else an inverse shift in the silences. Each person has his own rate of adjustment, defined by the position of the curve in relation to the intercepts.

If the *b* and *d* slopes represent processes of formation of durations at

different rates, the function (2) indicates that these processes are united in a single system, the limits of which are those cases in which at a given ratio of the $b$ slopes, either the actions or the silences have reached a limit beyond which no $d$ slope is formed. Thus the range between the upper and lower limits of the appearance of two $d$ slopes defines the capacity of the individual to vary his $d$ rates, evidenced by the appearance of $d$ slopes. But the variation of rates so occurring is due to the process of adjustment to an individual with whom a specific individual is interacting. It can easily be seen that if neither individual interrupts the other, and if neither one is silent when the other is silent, the actions of one person will equal the silences of the other, and, conversely, and the slopes of the frequency distributions will be the same. By examination of the evidence (to be published in another place), it can be seen that this occurs very rarely. Nevertheless, there has to be a certain degree of adjustment unless one individual only talked when the other talked and was silent when the other was silent. Therefore, within the limits of adjustment of the action slopes of individual $A$ to $B$'s silences and, conversely, the values of the $d$ slopes have to be determinate. From this it follows that, in a first approximation, the limits of the appearance of a $d$ ratio defines the capacity of an individual to vary his $d$ rate in adjustment to another individual. An individual like $KY$ or $JOB$, exhibiting a very narrow range of $d$ ratios, is a person whose variation in response to others is such that within only a narrow range of adjustment can they manifest the long values which produce the $d$ slope. The conditions of this adjustment will be dealt with at another time.

*Summary.*—The measurement of the interaction of individuals provides us with an opportunity to find out whether any unique property of an individual, ordinarily called "personality," manifests itself when two people are talking together. When a series of observations is made, the frequency distributions of the durations of action and silence are fitted by the exponential equation, $F = ae^{-bt} + ce^{-dt}$, and the plot of $\log b_a/b_s = -\log d_a/d_s$ with a slope of 1. The position of this curve as defined by the intercepts is invariant for each individual, since it does not shift when the individual interacts with different individuals. The range of the curve also may be invariant for each individual, being delimited at the lower end by the absence of a $d$ silence slope and at the upper end by the absence of a $d$ action curve. These invariant properties afford us a quantitative description of individual differences in "personality" as exhibited in the rates of acting and being silent in interaction.

[1] Allport, G. W., *Personality: A Psychological Interpretation*, New York, Holt, 1937; Cattell, R. B., *Brit. Jour. Psychol.*, **23**, 308; **24**, 20 (1933), afford examples of this procedure.

[2] Kretschmer, E., *Physique and Character* (trans. by W. J. H. Sprott), 2nd ed.,

London: Kegan Paul, 1936; Jung, C. G., *Psychological Types*, New York, Harcourt Brace, 1923, are well-known examples of this approach.

[3] Chapple, E. D., *Proc. Nat. Acad. Sci.*, **25**, 2, 1939.

[4] Crozier, W. J., and Hoagland, H., "The Study of Living Organisms," in Murchison, C., *A Handbook of General Experimental Psychology*, Worcester, Mass., Clark University Press, 1934, p. 3 and ff.

[5] Crozier, W. J., and Holway, A. H., *Jour. Gen. Physiol.*, **23**, 101 (1939).

[6] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **22**, 311 (1939).

[7] Chapple, E. D., *Measuring Human Relations* (to be published) for a discussion of this point.

[8] Made for us by C. A. Marston Co., Braintree, Mass.

[9] Lipka, J., *Graphical and Mechanical Computation*, p. 156 and ff., New York, Wiley, 1918.

[10] The author is greatly indebted to Gordon Donald for his assistance in calculating these slopes.

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## *THE NATURE OF ABSORPTION OF RADIOACTIVE ISOTOPES BY LIVING TISSUES AS ILLUSTRATED BY EXPERIMENTS WITH BARLEY PLANTS*[1]

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*Introduction.*—In a recent article Jenny and Overstreet[2] proposed a theory of ionic interchange between plant roots and soil colloids based on the assumption of partial interpenetration of the ionic double layers of root and clay surfaces. In the development of this theory of "contact exchange" the outgo of radioactive potassium from barley roots into clay suspensions and salt solutions was studied. It was found that the radioactive isotope moved readily from the roots into colloidal clay suspensions saturated with monovalent cations and to a much lesser degree into those saturated with divalent cations. This outward movement did not occur with distilled water, or with certain salt solutions investigated, of ionic content comparable to that of the colloid, with the notable exception of solutions of potassium salts. Radioactive potassium was found to move readily from barley roots into both clay suspensions saturated with potassium and solutions of potassium salts. Outward movement of radioactive potassium occurred simultaneously with the accumulation by the roots of non-radioactive potassium. This two-way movement of potassium between the roots and the bathing solutions has been interpreted as evidence for the existence of ionic exchange of cations. In this paper a more detailed examination is made of the factors governing the movement of radioactive cations between culture solutions and plant roots.

Let us consider the equilibrium distribution of any strong electrolyte $A\,B$ in an inanimate system consisting of $n$ phases. If the $A\,B$ molecule dissociates into $\nu$ ions where $\nu = \nu_A + \nu_B$ ($\nu_A$ = no. of cations; $\nu_B$ = no. of anions), then the equilibrium condition for *all phases* is:

$$(a_A^{\nu_A} \times a_B^{\nu_B})_{n_1} = (a_A^{\nu_A} \times a_B^{\nu_B})_{n_2} = \ldots\ldots = k. \qquad (1)$$

$a_A$ and $a_B$ are the activities of the cation and anion, respectively, and $k$ is a constant. In the system under consideration it is assumed that the phase boundaries are permeable to all ions. However, equation (1) also has been applied to a very important class of systems in which one or more of the cations or anions are impermeable to the phase boundaries (Donnan Equilibrium). Obviously in such systems $A\,B$ refers to permeable electrolytes.

If one of the cations $A$ in the above system is a mixture of several isotopes $A_1$, $A_2$, $A_3$, etc., which in any phase have the isotopic mol fractions $N_{A_1}$, $N_{A_2}$, $N_{A_3}$, etc., at equilibrium the distribution of the isotopes will be such that:

$$\begin{aligned} (N_{A_1})_{n_1} &= (N_{A_1})_{n_2} = \ldots\ldots = k_1, \\ (N_{A_2})_{n_1} &= (N_{A_2})_{n_2} = \ldots\ldots = k_2, \\ (N_{A_3})_{n_1} &= (N_{A_3})_{n_2} = \ldots\ldots = k_3. \end{aligned} \qquad (2)$$

A distinguishing characteristic of systems in which one or more of the phases are embodied in living tissue (plant or animal cells) is the fact that the equilibrium condition represented by equation (1) rarely if ever obtains. The trend of life processes is usually away from this equilibrium condition. The accumulation of electrolytes from culture media by plant and animal cells is a well-known example of this.[3] On the other hand, the equilibrium distribution of isotopes represented by equations (2) is nearly always maintained in nature, even in those systems where one or more phases are present in living tissue. In general plant and animal cells are unable to bring about a separation of isotopes. From this fact it may be concluded that in the processes of metabolism and salt accumulation in plants, isotopes behave very nearly alike. The assumption seems safe that under natural conditions any plant-culture solution system is in a state of isotopic equilibrium. However, what trends may we expect if this equilibrium in such a system is deliberately disturbed, as for example by the addition of a radioactive isotope to the culture solution bathing the roots of a plant? This question is complicated by the fact that living systems are usually in a state far removed from that of thermodynamic equilibrium represented by equation (1). Jenny and Overstreet[2] have shown that the passage of cations between the culture medium and the root is not unidirectional (except as a net effect resulting in accumulation of cat-

ions under the influence of metabolic activities of the living cells). From this we may conclude that many if not all the phase boundaries in the plant are permeable to cations in both directions, although the permeability to an ion in one direction may be much greater than in the opposite direction. Consequently in the forementioned disturbed system, an undetermined number of phases within the plant would tend toward isotopic equilibrium with the culture medium. This would be expected even though the phases were not in thermodynamic equilibrium, since the phase boundaries are permeable to the radioactive ion in both directions. Furthermore, it is evident that the trend toward isotopic equilibrium between the culture medium and the plant root must involve a process of ionic exchange between isotopes. Thus the process is undoubtedly intimately linked to the ion exchange mechanisms of the plant. For this reason experiments were designed to observe this trend.

From the above considerations it follows that the entry of a radioactive isotope into plant roots from culture solutions will be governed by two major factors. First, the entry is dependent on the inward movement of the particular ion species to which the isotope belongs. For example, the entry of radioactive potassium is dependent on the total entry of potassium (radioactive and non-radioactive). Second, the influx is dependent on the distribution of the isotope in the various phases of the system. In other words, radioactive potassium initially in the culture solution would be expected to enter the root and move, by whatever means at its disposal, throughout the plant until the state of equal isotopic mol fractions in all phases concerned is attained. For these reasons, in order to study adequately the absorption of radioactive potassium by barley roots, it has been necessary to study the absorption of all forms of potassium.

*Experimental Technique.*—The experiments were conducted with barley plants of the Sacramento variety. The plants were grown according to the method of Hoagland and Broyer.[4] They are characterized by a relatively low potassium content and the roots readily accumulate potassium from very dilute solutions. Barley seeds were germinated in special chambers and transplanted into shallow pans each of which contained 3800 cc. of nutrient solution. One hundred and sixty-eight plants were set out in each pan in 24 corks. The volume of solution in the pans was maintained by the addition of distilled water daily. After approximately 3 weeks the barley plants, which had grown to about 18 inches in length, showed the first signs of starvation in the shoot, but the roots were entirely healthy ("low-salt" plants). At this stage the plants were used for experimentation. In the experiment reported here decapitated plants were used; that is, the shoots were cut off one inch above the root-stem plate. The culture solutions were analyzed for radioactivity by the method described by Jenny, Overstreet and Ayers.[5]

*Experimental Data.*—In the first experiment the uptake of radioactive potassium by the "low-salt" plants was studied. Groups of 84 decapitated plants were placed in shallow pans each of which contained 3000 cc. of 0.0005 *N* KCl. The KCl contained radioactive potassium, the radioactivity of the dry salt in one liter of solution being of the order of one microcurie. The plants were left in the aerated culture solutions for periods up to 9 hours. At the conclusion of each absorption period the 84 plants were removed and suitable aliquots of the culture solution were tested for radioactive potassium and analyzed for total potassium. The

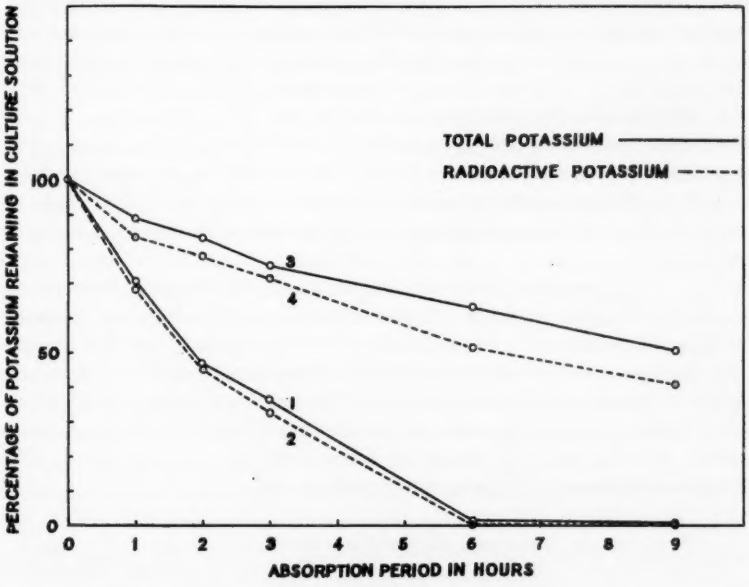


FIGURE 1

radioactive potassium and total potassium contents were each expressed as the percentages of the radioactive potassium and total potassium contents of the original culture solution. These percentages are plotted against the absorption times in figure 1, curves 1 and 2. The graph shows that the fractional uptake of the radioactive isotopes is not significantly different from that of the non-radioactive isotopes. No trend toward isotopic equilibrium can be detected with the "low-salt" plants since the capacity for accumulation of all kinds of potassium is so large. It is apparent from curves 1 and 2, figure 1, that the plant cannot distinguish between radioactive and non-radioactive isotopes in absorption, within the limits of error of this experiment.

From the data of the foregoing experiment it seemed probable that in order to observe the trend toward isotopic equilibrium it would be necessary to reduce the total accumulation of potassium. With this point in view the following experiment was run. "Low-salt" barley plants were allowed to absorb salt for a period of 19 hours from a nutrient solution containing a relatively high amount of non-radioactive potassium. During this period the potassium content of the roots rose from 34.7 to 131 milliequivalents per 100 grams oven-dry material (the average oven-dry weight of the roots from 84 plants was 3.75 grams). The shoots were then cut off and groups of 84 plants allowed to absorb KCl containing radioactive potassium under exactly the same conditions as in the first experiment. The percentages of total and radioactive potassium remaining in the culture solution are plotted in figure 1, curves 3 and 4. Examination of the curves reveals that the pretreatment has greatly reduced the rate of accumulation of total potassium as well as the accumulation of radioactive potassium. The significant divergence of curves 3 and 4 shows that the pretreated plants exhibit a preferential absorption of the radioactive isotope. This would be expected from the considerations mentioned above in regard to isotopic equilibrium.

An attempt was then made to produce roots which would show no increase in total potassium when immersed in dilute KCl solutions containing radioactive potassium. Under these conditions the only possible absorption reaction would be an ionic exchange between potassium of the culture solution and potassium of the root. To this end, barley plants were grown for 3 weeks in complete nutrient solution which was renewed 3 times a week. The decapitated plants were then immersed in radioactive KCl solutions as before. The results are given in table 1.

TABLE 1

ABSORPTION OF K FROM 0.0005 *N* KCl SOLUTIONS (3 LITERS) CONTAINING $K^{*6}$ BY DECAPITATED "HIGH-SALT" BARLEY PLANTS

| ABSORPTION PERIOD IN HOURS | % OF ORIGINAL K REMAINING IN CULTURE SOLUTION | % OF ORIGINAL K* REMAINING IN CULTURE SOLUTION | RADIOACTIVITY OF DRY ASH OF ROOTS IN COUNTS PER MIN. |
|---|---|---|---|
| 0 | 100.0 | 100.0 | 0 |
| 1 | 112.2 | 95.7 | 136 |
| 2 | 110.8 | 97.3 | 167 |
| 3 | 110.8 | 91.0 | 269 |
| 6 | 109.9 | 93.7 | 278 |
| 9 | 119.4 | 91.0 | 629 |

Average oven-dry weight of roots from 84 plants = 2.65 gm.
Original total K content of roots of 84 plants = 0.145 gm.

Table 1 reveals the following facts. The "high-salt" roots actually decreased in total potassium, yielding potassium to the culture solutions. At the same time the roots absorbed radioactive potassium. This absorption

of radioactive potassium by the roots is brought out more significantly by the counts on the dry ash of the roots. The results are shown in the fourth column of table 1, in which the counts per minute on the dry ash of each set of 84 plants are given. There occurred a continuous exchange of radioactive potassium of the culture solution for non-radioactive potassium of the root throughout the 9-hour absorption period. The question arises now as to the extent to which this simple exchange process between culture solution and plant would go if given longer periods of time. It is possible that eventually all parts of the plant would come to isotopic equilibrium with the culture solution, but certain experiments with barley plants at low temperatures indicate that, at least for those conditions, such isotopic equilibrium may never be reached within the life period of the tissues. At 0°C. barley plants accumulate potassium from KCl solutions in very minute amounts if at all. On the other hand, it has been found in another research (Broyer and Overstreet) that the exchange of radioactive potassium between plant roots and culture solution is little affected by temperature. Thus for even "low-salt" barley plants placed in dilute KCl solutions containing radioactive potassium, the major process occurring at low temperatures is a simple exchange of radioactive potassium of the culture solution for ordinary isotopes of potassium initially present in the plant. In an experiment to be reported more fully elsewhere (Broyer and Overstreet) sets of 7 barley plants each were placed in 400 cc. of 0.000455 *N* KCl solution containing radioactive potassium at 0°C. After various absorption periods from $^1/_2$ minute to 3 hours the roots were removed from the culture solution, washed, ashed and counts for radioactivity made. The results are shown in figure 2 in which the counts per minute for the roots of the seven plants are plotted against the absorption time. The absorption of radioactive potassium tended toward a maximum indicating that under these conditions only a limited part of the plant may be involved in the exchange process.

*Discussion.*—The experiments show that "low-salt" barley plants (containing approximately 30 milliequivalents potassium per 100 gm. dry weight of roots) at normal temperature absorb radioactive potassium and non-radioactive potassium from culture solutions in very nearly constant proportions. These plants apparently do not distinguish between the radioactive and non-radioactive isotopes in absorption from solutions of the concentrations indicated, but barley plants of high potassium level definitely do not absorb the isotopes in constant proportions. With these latter plants, the absorption of the radioactive isotope is favored. This fact is in harmony with the picture of a trend toward isotopic equilibrium between the culture solution and plant roots.

The trend toward isotopic equilibrium involves in essence a simple exchange between radioactive isotopes of the outside medium for non-radio-

active isotopes of the plant. If we assume the plant root to include a system of colloidal particles possessing adsorbed potassium ions, the process may be indicated by the equation:

$$\boxed{\begin{matrix}\text{Colloidal}\\ \text{particle}\end{matrix}}\begin{matrix}K\\ K\\ K\end{matrix} + K^*Cl = \boxed{\begin{matrix}\text{Colloidal}\\ \text{particle}\end{matrix}}\begin{matrix}K^*\\ K\\ K\end{matrix} + KCl. \qquad (3)$$

As may be seen from equation (3), the reaction involves no change in the total amount of potassium adsorbed on the colloidal particles. This phenomenon presents a serious difficulty in the quantitative interpretation of data concerning radioactive elements, which becomes apparent from the data cited on experiments with potassium ions. For example, in one instance (Fig. 1, curves 3 and 4) both radioactive and non-radioactive potassium enter the plant in proportions which vary with time, while in another instance (Fig. 2) there is a movement of radioactive potassium into the plant with no *net* movement of potassium in the plant-solution culture system. A still more striking case is described in table 1, in which a movement of radioactive potassium into the plant is accompanied by a net release of potassium from the plant. In the light of the above information it seems imperative that conclusions in regard to net movements of an ion initially present in the organism based on observations of the movements of its radioactive isotope must be made with caution. This is especially true in the absence of information on the movements of the non-radioactive isotopes, and on the original salt status of the living material. The absorption of radioactive ions, while of great interest in relation to intermediate steps in the process of net accumulation of ions involving metabolically controlled cell activities is not a measure of this accumulation.

Experiments with barley roots indicate that under low temperature conditions only a certain part of the root is capable of attaining isotopic equilibrium with the outside medium within moderate time periods. This part may represent the colloidal phases of the protoplasm and cell wall which are capable of rapid ionic exchange with the outside solution. It is of interest to calculate the total potassium associated with this fraction from the data for figure 2. At the maximum of the curve, 1350 counts for the roots of 7 plants, it will be assumed that a certain fraction of the potassium of the roots is in isotopic equilibrium with the potassium of the culture solution. Thus for the two quantities of potassium involved, the ratio of radioactive potassium to total potassium must be the same. At the equilibrium point the outside culture solution contained 7.11 mg. potassium and the total count of radioactivity on a basis comparable to that used in estimating radioactivity in the roots was 50,900 counts per minute. From these data it follows that 0.188 mg. of the total potassium present in the seven plants is capable of isotopic equilibrium with the outside solution.

Since the oven-dry weight of the roots of seven plants was 0.17 gm. this potassium corresponds to about 2.8 milliequivalents per 100 gm. of the oven-dry roots. The total potassium content of the roots was approximately 30 milliequivalents per 100 gm. of oven-dry material. Consequently, roughly 10% of the total potassium in the roots of "low-salt" barley plants is exchangeable at 0°C. Since the effect of temperature upon the exchange reaction is known to be slight, this percentage can be assumed to represent that fraction of potassium in the roots at normal temperatures which is capable of rapid exchange for isotopes in the bathing culture medium. This value has the same order of magnitude as that for potassium

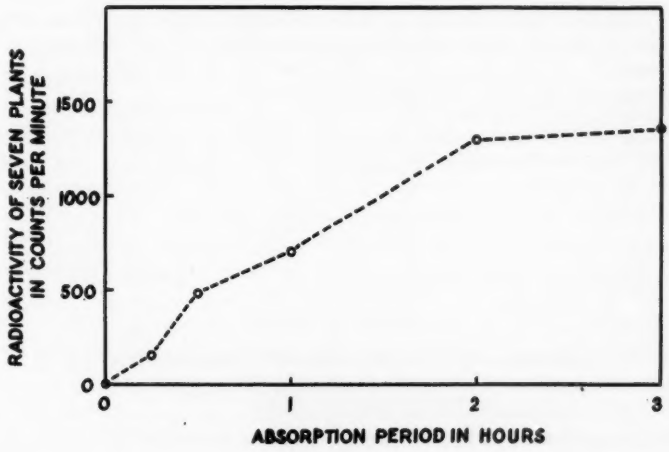


FIGURE 2

not easily recoverable by sap expression methods (unpublished data, Broyer and Hoagland).

*Summary.*—From considerations of equilibria, it is concluded that plant roots may absorb radioactive ions by means of a simple exchange of radioactive isotopes of the surrounding culture medium for non-radioactive isotopes initially present within the plant.

Barley plants with low potassium levels absorb radioactive and non-radioactive isotopes of potassium in nearly constant proportions from dilute KCl solutions in which the radioactivity of the dry salt is of the order of one microcurie per liter. Under similar conditions, barley plants with moderately high potassium levels favor the radioactive isotope in absorption.

Under the conditions studied, plants with high potassium levels or plants maintained at low temperatures do not show a net absorption of potassium. However, they do absorb radioactive potassium, indicating a process of

exchange of radioactive isotopes in the culture medium for non-radioactive isotopes in the roots.

The fraction of potassium present in the root capable of rapid exchange for isotopes in the culture medium is calculated. This fraction is believed to be associated with the colloidal phases of the protoplasm and cell wall, and for this reason may have a special significance for the study of certain aspects of the ionic interrelations of the root and culture medium.

*Acknowledgments.*—The authors are indebted to Professors D. R. Hoagland and H. Jenny for their interest and valuable suggestions, and to Professor E. O. Lawrence, Director of the Radiation Laboratory, for supplying radioactive potassium.

[1] Assistance in the preparation of the experimental material was furnished by the personnel of Works Progress Administration Official Project No. 465-03-3-587.

[2] Jenny, H., and Overstreet, R., *Proc. Nat. Acad. Sci.*, **24**, 384 (1938).

[3] Compare Brooks, S. C., *Protoplasma*, **8**, 389 (1929).

[4] Hoagland, D. R., and Broyer, T. C., *Plant Physiol.*, **11**, 471 (1936).

[5] Jenny, H., Overstreet, R., and Ayers, A. D., *Soil Sci.*, **48**, 9 (1939).

[6] The star is used to designate the radioactive isotope of potassium.

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## *CONCERNING THE OPEN SUBSETS OF A PLANE CONTINUUM*

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In this paper, two theorems relating to unbounded plane continua will be established.

THEOREM 1. *If, in a plane $S$, $K$ is a closed point set and $G$ is a countable set of mutually exclusive continua and $G^*$ (the sum of all the continua of the set $G$) has no point in common with $K$ and $G^* + K$ is a continuum then every element of $G$ is a component of $G^*$.*

*Proof.* Let $M$ denote $G^* + K$. Suppose $K$ has a bounded component $H$. Then there exists a bounded domain $D$ containing $H$. Let $L$ denote the component of $M \cdot \overline{D}$ that contains $H$. The boundary of $D$ contains a point $B$ of $L$. Thus the connected subset $L$ of $M$ contains at least one point $B$ not belonging to $H$. Hence $L$ is not a subset of $K$. Let $W$ denote the collection whose elements are $K$ and the continua of the set $G$. Let $Q$ denote the set of all point sets $q$ such that $q$ is the common part of $L$ and some point set of the collection $W$. The collection $Q$ is a non-degenerate countable collection of mutually exclusive closed point sets filling up the compact continuum $L$. But this is contrary to a theorem of Sierpinski's.[1] It follows that every component of $K$ is unbounded.

If there were only one continuum in the collection $G$ then $M$ would be the sum of two mutually exclusive closed point sets $K$ and $M$-$K$, contrary to the supposition that it is a continuum. Hence there exist two continua $x$ and $y$ belonging to $G$. There exists an arc $AB$ from a point $A$ of $x$ to a point $B$ of $y$. With the aid of the above-mentioned theorem of Sierpinski's, it follows that $AB$ contains a point $O$ not belonging to $M$. Let $T$ denote an inversion of the plane $S$ about some circle with center at $O$. Let $g$ denote a continuum of the collection $G$ and let $N$ denote the component of $M$-$K$ that contains $g$. Suppose $N$ is distinct from $g$. Then there exists an infinite subcollection $G_1$ of $G$ such that $N$ is the sum of all the continua of $G_1$. The point set $T(N)$, the image of $N$ under the inversion $T$, is bounded and connected. Since every component of the closed point set $K$ is unbounded, $O + T(K)$ is a compact continuum. Let $I$ denote the complementary domain of $O + T(K)$ that contains $T(N)$. The boundary of $I$ is a subcontinuum $\beta$ of $O + T(K)$ and $T(N) + \beta$ is closed. There exists a reversibly continuous transformation $Z$ throwing the simply connected domain $I$ into the plane $S$. The image of $T(N)$ under this transformation is a plane continuum which is the sum of a countable number of mutually exclusive continua. But this involves a contradiction.[2] It follows that $N$ is identical with $g$ and, therefore, that every element of $G$ is a component of $M$-$K$.

It has been shown by W. T. Reid[3] that if $K$ is a proper subcontinuum of a plane continuum $M$ then $K$ contains a limit point of some component of $M$-$K$. This proposition does not remain true if the requirement that $K$ be a proper subcontinuum of $M$ is replaced by the weaker requirement that it be a closed subset of $M$. Indeed the following theorem holds true.

THEOREM 2. *There exists a plane continuum $M$ containing a closed point set $K$ such that $M$-$K$ has only a countable number of components and $K$ contains no limit point of any one of them.*

*Proof.* It has been shown by Mazurkiewicz[4] that there exists a plane continuum $M$ which is the sum of a countable number of mutually exclusive closed point sets all but one of them being continua. Let $K$ denote the one which is not a continuum and let $G$ denote the collection of all the others. By Theorem 1, every continuum of the collection $G$ is a component of $M$-$K$. But $K$ contains no limit point of any continuum of that collection.

[1] W. Sierpinski, "Un theoreme sur les continus," *Tohoku Math. Jour*, **13**, 300–303 (1918).

[2] That no plane continuum is the sum of a countable number of mutually exclusive continua has been shown both by Mazurkiewicz and by the author. Cf. *Fundamenta Mathematicae*, **5**, 188–205 and **6**, 189–202.

[3] "A Theorem on Plane Continua," *Bull. Amer. Math. Soc.*, **41**, 684–688 (1935).

[4] Loc. cit.

# ON HOMOTOPY AND EXTENSION OF MAPPINGS

By Ralph H. Fox

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Communicated November 25, 1939

The purpose of this note is to exhibit a relation between certain special homotopy properties and the problem of extending mappings.[1] We consider only separable regular spaces, i.e., homeomorphs of subsets of the Hilbert parallelotope. Mapping means continuous mapping.

THEOREM. *If $A$ is a compact set and $Y$ is an absolute neighborhood retract then a necessary and sufficient condition for a mapping $f \in Y^A$ to be homotopic to a constant is that $f$ be extendable* (relative to $Y$) *to every space $X$ which contains $A$.*

Since a constant mapping can be extended to every space $X$ the necessity is a consequence of the theorem. *If mappings $f$ and $g \in Y^A$ are homotopic then, for any $X$ containing $A$, $f$ can be extended to $X$ if and only if the same is true of $g$.* Interpreting homotopy of $f$ and $g$ as the existence of a continuous curve in $Y^A$ containing $f$ and $g$, this is easily seen to be a consequence of the Borsuk theorem.[2] *The set $\Pi(Y^A, X)$ of mappings of $Y^A$ which can be extended to $X$ is open and closed in $Y^A$.*

The proof of the sufficiency of this condition does not require anything of the separable, regular spaces $A$ and $Y$. Let $X$ be the Hilbert parallelotope so that by hypothesis there is a mapping $f^* \in Y^X$ such that $f^*(x) = f(x)$ for every $x \in A$. Since $A$ is contractible in $X$ there is a mapping $h \in X^{A \times [0,1]}$ and a point $p \in X$ such that $h(x, 0) = p$ and $h(x, 1) = x$. Then $f^*h \in Y^{A \times [0,1]}$ and $f^*h(x, 0) = f^*(p) \in B$ and $f^*h(x, 1) = f^*(x) = f(x)$. Thus $f^*h$ is a homotopy in $Y$ between $f$ and a constant.

By specializing $A$ to a subset $B$ of $Y$ and $f$ to the identity we have

COROLLARY. *If $B$ is a closed subset of an absolute neighborhood retract $Y$ then $B$ is contractible in $Y$ if and only if for every space $X$ containing $B$ there is a mapping $f^* \in Y^X$ under which every point of $B$ is fixed.*

An equivalent formulation is easily seen to be the following:

*If $B$ is a closed subset of an absolute neighborhood retract $Y$ then $B$ is contractible in $Y$ if and only if for every space $X$, closed subset $A$ and mapping $f \in B^A$ there is an extension of $f$ to $X$ relative to $Y$.*

Further specializing $A$ to be equal to $Y$ yields the classical theorem.[2]

*In order that an absolute neighborhood retract be contractible it is necessary and sufficient that it be an absolute retract.*

Obviously the corollary permits one to replace any statement about sets contractible in an absolute neighborhood retract $Y$ by a statement about fixed points under mappings into $Y$. Thus in particular

*The category,*[1] *cat Y, of an absolute neighborhood retract Y imbedded in the Hilbert parallelotope X is the least integer k for which there are k mappings* $f_1, f_2, \ldots, f_k \in Y^X$ *such that every point of Y is fixed under one of these mappings.*

This result, which might serve as the definition of category, is of particular interest as it exhibits the category as a generalization of the notion of absolute retract.

An equivalent formulation is the following generalization of a Borsuk theorem.[3]

*The category, cat Y, of an absolute neighborhood retract Y is the least integer k such that, given any space X and closed subset A and mapping* $f \in Y^A$, *there are k mappings* $f_1, f_2, \ldots, f_k \in Y^X$ *such that for every* $x \in A$ *there is an index i for which* $f_i(x) = f(x)$.

Elsewhere,[4] I have introduced the concept of $n$-homotopy. Mappings $f$ and $g \in Y^A$ are said to be *n-homotopic* if the continuous complexes $f\phi$ and $g\phi \in Y^P$ are homotopic for every at most $n$-dimensional continuous complex $\phi \in A^P$. I have raised the question[5] of the extendability of a mapping which is $n$-homotopic to an extendable mapping. Our only theorem in this connection concerns the converse problem.

*If A is a compact set and f is a mapping* $\in Y^A$, *a sufficient condition for f to be n-homotopic to a constant is that f be extendable to every at most* $(n + 1)$*-dimensional compact space X which contains A.*

According to Borsuk[6] there is an $(n + 1)$-dimensional infinite complex $P_{n+1}$ such that $X = A + P_{n+1}$ is compact and $LC^n$ and every at most $n$-dimensional continuous complex in $X$ is homotopic to a constant. Hence the identity mapping, 1 of $A$ is $n$-homotopic in $X$ to a constant. If $f^*$ is an extension of $f$ to $X$ then $f^*1 = f$ is $n$-homotopic in $Y$ to a constant.

Returning to the situation in the second formulation of the corollary we consider spaces $X$ and $Y$ and a mapping $f$ of a closed subset $A$ of $X$ into a subset $B$ of $Y$. We have found conditions under which the existence of an extension $f^*$ of $f$ to $X$ relative to $Y$ is assured. We shall now look for conditions which guarantee the existence of an $f^*$ which has the additional property that it maps $X - A$ into $Y - B$. Such an extension has been called, by Lefschetz,[7] an *expansion.* The use which Lefschetz makes of expansion rests on the following remark:

*If f and g are mappings* $\in B^A$, $f^*$ *is an expansion of f to X relative to Y and* $g^*$ *is an extension of g to X relative to B then* $f^*$ *and* $g^*$ *have the same coincidences as f and g.* Explicitly: $f(x) = g(x)$ *if and only if* $f^*(x) = g^*(x)$.

When $Y$ is the unit segment [0, 1] and $B$ is the union [0] + [1] of its endpoints, any $f$ has an expansion[8] given by

$$f^*(x) = \frac{\rho(f^{-1}(0), x)}{\rho(f^{-1}(0), x) + \rho(x, f^{-1}(1))},$$

where $\rho$ is a metric in $X$.

To prove a general theorem on expansion we introduce the following terminology: $A$ subset $B$ of a space $Y$ is *deformable* in $Y - B$ if there is a mapping of the cylinder $B \times [0, 1]$ into $Y$ which leaves every point of $B = B \times [0]$ fixed and maps the remainder $B \times (0, 1]$ into $Y - B$. If, in addition, $B \times [1]$ is mapped into a single point, $B$ will be said to be *contractible* in $Y - B$.

*A necessary and sufficient condition for a subset $B$ of a space $Y - B$ to be deformable in $Y - B$ is that for every space $X$ and retract $A$ of $X$ any mapping $f \in B^A$ can be expanded to $X$* (relative to $Y$).

The sufficiency of the condition follows from the definition of deformation in $Y - B$ on choosing $X = B \times [0, 1]$ and $A = B \times [0]$.

To prove the necessity we define the following functions:

(*a*) $r \in A^X$ such that $r(x) = x$ for every $x \in A$.

(*b*) $h \in Y^{B \times [0, 1]}$ such that $h(y, 0) = y$ and $h(y, t) \in Y - B$ for every $(y, t) \in B \times (0, 1]$.

(*c*) $u \in [0, 1]^X$ such that $u^{-1}(0) = A$; $u$ may be defined explicitly by $u(x) = \lambda\rho(x, A)$ with $\lambda$ a suitable positive number. We then define $f^* \in Y^X$ by

$$f^*(x) = h(f(r(x)), u(x))$$

and observe that $f^*$ is the desired expansion.

Slight modification of the previous proof is all that is required to obtain either of the following two theorems:

*A necessary and sufficient condition for a subset $B$ of a space $Y$ to be contractible in $Y - B$ is that for every space $X$ and neighborhood retract $A$ of $X$ any mapping $f \in B^A$ can be expanded to $X$* (relative to $Y$).

*A necessary and sufficient condition for a subset $B$ of a space $Y$ to be deformable in $Y$ into another subset $B'$ is that, for every space $X$, retract $A$ of $X$ and neighborhood $U$ of $A$ in $X$, any mapping $f \in B^A$ has an extension $f^* \in Y^X$ such that $f^*(X - U) \subset B'$.*

[1] For the terms used the reader is referred to the papers of Borsuk, especially *Fund. Math.*, **17**, 152–170 (1931); **19**, 220–242 (1932); **26**, 123–136 (1936).

[2] *Fund. Math.*, **19**, 229.

[3] *Fund. Math.*, **17**, 161.

[4] "On the Lusternik Schnirelmann Category," to appear in *Ann. Math.*, §13.

[5] *Ibid.*, §20.

[6] *Fund. Math.*, **27**, 242 (1936).

[7] Topology (1930), 287.

[8] Compare Vedenissoff, *Fund. Math.*, **27**, 234–238 (1936).

# INTEGRATION AND DIFFERENTIATION IN PARTIALLY ORDERED SPACES

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We consider a vector space $S$ which is partially ordered (relation $>$). By definition, $S$ is an Abelian group of addition with the ring of real numbers as coefficients (operators), and corresponding to any two elements $a$, $b$ of $S$ there exists a unique element sup $(a, b)$ and a unique element inf $(a, b)$. As usual, sup $(a, 0)$ − inf $(a, 0)$ will be denoted by $|a|$. We assume that $S$ is complete: every set of elements $A$ which is bounded from above (below) has a sup (inf). This leads to a sequential limit topology is $S$. Namely, $a_n \to 0$ if

$$\inf_n \sup (|a_n|, |a_{n+1}|, \ldots) = 0. \tag{1}$$

In this connection we introduce elements $+\infty$ and $-\infty$ with properties stated by L. V. Kantorovitch.[1] A concept of limit which requires more than (1) is dominated convergence; it requires the existence of an element $a_o > 0$ such that $|a_n| \leq \epsilon a_o$ for $n \geq N(\epsilon)$, $\epsilon$ real. However, Kantorovitch has shown that convergence is equivalent with dominated convergence if the following axiom is fulfilled.

*Axiom* $(K)$. If $A_m$ $(m = 1, 2, \ldots)$ is a set of elements of $S$ which is bounded from above then there exists a finite subset $A'_m$ such that

$$\lim_{m\to\infty} \sup A'_m = \lim_{m\to\infty} \sup A_m$$

if the limit on the right hand exists.

We will later add another axiom. However, we will not make the assumption that our space has a Banach norm. For the construction of a Lebesgue theory of integration the Banach norm can be replaced by axiom $(K)$. We consider a countably additive Boolean algebra of sets $E$ of an arbitrary space $B$ and a countably additive numerical measure $\mu E$ on it, and we make the assumption that $B$ is also measurable and that $\mu B$ is finite. We call a sequence of functions $f_n(t)$ from $E$ to $S$ uniformly convergent to $f(t)$ if there exists a sequence of element $a_n \to 0$ such that $|f_n(t) - f(t)| < a_n$, and we call it *convergent in measure* if for any numerical $\epsilon > 0$ there exists a subset $E_o$ of $E$ such that $\mu(E - E_o) < \epsilon$ and $f_n(t)$ converges uniformly on $E_o$. A step function $s(t)$ on $E$ is one which has a constant value $a_\nu$ on each set $E_\nu$ of a finite partition of $E$, and the integral $\int s(t)d\mu$ on $E$ is the sum $\Sigma a_\nu \mu E_\nu$. We now call a function $f(t)$ measurable if it is the limit in measure of a sequence of step functions $s_n(t)$; we call it integrable if the integral of the double sequence $|s_m - s_n|$ tends to 0; and we

define the integral of $f(t)$ as the limit of the integral of $s_n(t)$. At this juncture axiom $(K)$ plays its rôle: a limit in measure of measurable functions is again measurable; the value of $\int f(t)d\mu$ is independent of the approximating sequence $s_n(t)$; furthermore, if a measurable function is dominated by an integrable function, it is also integrable and if a dominated sequence converges in measure then the integral of the limit is the limit of the integral. It is important to note that convergence in measure implies convergence almost everywhere and that we are making no statement about the converse.

An additive set function $F(E)$ from $B$ to $S$ is absolutely continuous if there exists an error function $e(\eta)$ from real numbers to $S$, which tends to 0 with $\eta$ such that $|F(E)| \leq e(\mu E)$. The indefinite integral of an integrable function is absolutely continuous, however the converse is not true. In the case of Banach spaces satisfactory criteria for $S$ are known under which the converse if valid.[2] As for our partially ordered spaces, we will not give a complete discussion but state one criterion for sufficiency. We will say that $S$ has the property $(D)$ if every absolutely continuous function is an indefinite integral. $S$ having the property $(D)$ does not depend on the Boolean algebra provided no set of positive measure is indivisible; and it is equivalent with the property of every monotone function $f(t)$ from the real interval $0 \leq t \leq 1$ to $S$ having a finite derivative almost everywhere. From this equivalence it can be seen that property $(D)$ is implied by the following axiom, which for instance is fulfilled for the ordinary $L_p$ spaces, $p > 1$.

*Axiom* $(L)$. There exists on $S$ a countable number of numerical additive functionals $\alpha_n = L_n(a)$, each of which is non-negative for positive $a$ and continuous in the sequential topology of $S$, such that $L_n(a) > 0$ for all $n$ implies $a > 0$ and that, for $a_1 \leq a_2 \leq \ldots$, $\lim_{m \to \infty} L_n(a_m) < +\infty$ for all $n$ implies $\sup a_m < +\infty$.

Axiom $(L)$ allows us to generalize many other theorems none of which have been known for Banach spaces. The most interesting is Birkhoff's *strong ergodic theorem:* if $f(t)$ is an integrable function with period 1 from real numbers to $S$ then

$$\frac{1}{n} \sum_{\nu=1}^{n} f\left(t + \frac{\nu}{n}\right)$$

has a limit as $n \to \infty$ for almost all $t$. Furthermore if

$$\sum (a_n \cos 2\pi nt + b_n \sin 2\pi nt)$$

is the Fourier series of $f(t)$ and $f(t)$ satisfies a Lipschitz condition of order $> 1/2$ (in particular if $f(t)$ has a bounded derivative) then

$$\sum (|a_n| + |b_n|) < +\infty. \qquad (2)$$

Finally, if $f(t)$ is an almost periodic function and if all exponents $\lambda_n$ which occur in its Fourier series

$$\sum(a_n \cos \lambda_n t + b_n \sin \lambda_n t)$$

are linearly independent then (2) holds again.

[1] "Lineare halb-geordnate Raume," *Recueil mathematique, Moscou*, **2**, 121–168 (1937).

[2] For the literature see B. J. Pettis, "Differentiation in Banach spaces," *Duke Jour.*, **5** (1939).

[3] A. Zygmund, Trigonometrical series, p. 135.

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## *GALACTIC AND EXTRAGALACTIC STUDIES, III. PHOTOGRAPHS OF THIRTY SOUTHERN NEBULAE AND CLUSTERS*

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Approximately three-fourths of the external galaxies that are near enough for close classification are spirals, and most of the spirals can be easily placed in half a dozen common categories. Similarly the spheroidal galaxies are readily assigned to a few subtypes, rarely with abnormalities among them. The unusual forms, whether chaotically irregular like the Magellanic Clouds, or merely peculiar variations on the usual types of spiral and spheroidal galaxy, are, however, of uncommon interest and perhaps of special importance in the study of galactic structures and development.

Several instructive curiosities and abnormal forms are included among the nebulae and clusters represented on the following pages. Some have already been published by Harvard, or by other observatories, but most of them are here presented for the first time. With the exception of the reproduction in figure 2, all photographs were made with the 60-inch reflector at the Boyden Station, Bloemfontein. The scale is 26″ to the millimeter. Generally we have used Cramer High Speed emulsions, developing with rodinal. The reproduced photographs are selected from plates made in the regular course of work on clusters and nebulae; no particular pains were taken to obtain photographs specially suited to publication. As usual, the finer details are lost in the reproduction, but enough remains to indicate the peculiar importance of some of these objects and the advisability of further study, photometric and spectroscopic. In all figures North is at the top, West on the right, except for figure 1 for which West is at the top and South on the right.

In table 1 we have listed the principal objects of each photograph, giving coördinates and approximate magnification. The brief tabulated descriptions are amplified in the following comments on the individual figures.

1. The remarkable assembly of clusters and of bright and dark nebulosities that make up the Eta Carinae Nebula is too large for full exhibition by a single 60-inch reflector plate. The diameter is about 2°.5, and therefore less than a fifth of the area illuminated

TABLE 1

LIST OF REPRODUCED CLUSTERS AND NEBULAE

| FIGURE | NGC | R. A. (1900) h | m | DEC. ° | ′ | GALACTIC LONG. ° | LAT. ° | TYPE | ENLARGEMENT |
|---|---|---|---|---|---|---|---|---|---|
| 1 | $\eta$ Car | 10 | 41.2 | −59 | 09 | 255 | − 1 | Gaseous nebula | 2.0 |
| 2 | 6514 | 17 | 56.3 | −23 | 02 | 335 | − 2 | Trifid nebula | 0.9 |
| | 6523 | 17 | 57.6 | −24 | 23 | 334 | − 3 | Lagoon nebula | 0.9 |
| | 6531 | 17 | 58.6 | −22 | 30 | 335 | − 2 | Open cluster | 0.9 |
| 3 | 7793 | 23 | 52.7 | −33 | 07 | 330 | −79 | Spiral | 1.5 |
| 4 | 5236 | 13 | 31.4 | −29 | 21 | 283 | +31 | Spiral | 1.0 |
| 5 | 7582 | 23 | 12.9 | −42 | 54 | 314 | −67 | Spiral | 1.0 |
| | 7590 | 23 | 13.4 | −42 | 47 | 314 | −67 | Spiral | 1.0 |
| | 7599 | 23 | 13.8 | −42 | 48 | 314 | −67 | Spiral | 1.0 |
| 6 | 1097 | 2 | 42.1 | −30 | 41 | 193 | −64 | Barred spiral | 1.5 |
| 7 | 55 | 0 | 10.0 | −39 | 46 | 296 | −77 | | 1.0 |
| 8 | 5189 | 13 | 26.4 | −65 | 28 | 275 | − 4 | Gaseous nebula | 10.0 |
| 9 | 2442–3 | 7 | 36.6 | −69 | 18 | 248 | −21 | Barred spiral | 1.6 |
| 10 | 1566 | 4 | 17.8 | −55 | 11 | 231 | −43 | Spiral | 1.0 |
| 11 | 6753 | 19 | 03.0 | −57 | 12 | 307 | −26 | Spiral | 3.0 |
| 12 | 1559 | 4 | 16.4 | −63 | 02 | 241 | −41 | Barred spiral? | 1.5 |
| 13 | 6935 | 20 | 31.0 | −52 | 27 | 314 | −39 | Plate spiral | 1.5 |
| | 6937 | 20 | 31.4 | −52 | 30 | 314 | −39 | Plate spiral | 1.5 |
| 14 | 4782 | 12 | 49.3 | −12 | 02 | 273 | +50 | Double spheroidal | 2.4 |
| | 4783 | 12 | 49.4 | −12 | 03 | 273 | +50 | | |
| 15 | 2736 | 8 | 56.9 | −45 | 30 | 235 | + 1 | Streak nebula | 1.0 |
| 16 | 3581 | 11 | 07.7 | −60 | 46 | 259 | − 1 | Gaseous nebula | 1.6 |
| 17 | 3132 | 10 | 02.8 | −39 | 57 | 240 | +13 | Planetary | 3.4 |
| 18 | I 4662 | 17 | 37.2 | −64 | 38 | 296 | −19 | Magellanic type | 1.5 |
| 19 | 6438 | 17 | 52.9 | −85 | 25 | 275 | −27 | Spheroidal | 3.0 |
| | | 17 | 53.4 | −85 | 25 | 275 | −27 | Magellanic type | 3.0 |
| 20 | 4038–9 | 11 | 56.8 | −18 | 19 | 256 | +43 | Ring-tail spiral | 2.6 |
| 21 | 5139 | 13 | 20.8 | −46 | 57 | 277 | +14 | Globular cluster | 1.5 |
| 22 | 7099 | 21 | 34.7 | −23 | 38 | 355 | −48 | Globular cluster | 1.5 |
| 23 | 2818 | 9 | 12.0 | −36 | 12 | 230 | + 9 | Gaseous nebula in open cluster | 1.5 |

by bright nebulosity is shown in figure 1. A smaller scale photograph of the whole region, with the 24-inch Bruce reflector of the Boyden Station, is shown on the cover of *The Telescope* for May–June (1937). The section of the nebula here shown is the brightest part, and is most interestingly marked with sharp-edged dark streaks. The eighth magnitude star, Eta Carinae, which behaved like a nova a century ago and is now possessed of a peculiar bright-line spectrum, is located 2.4 cm. below the center of the photograph. On a red-sensitive plate this star is relatively conspicuous, but otherwise no

FIGURE 1

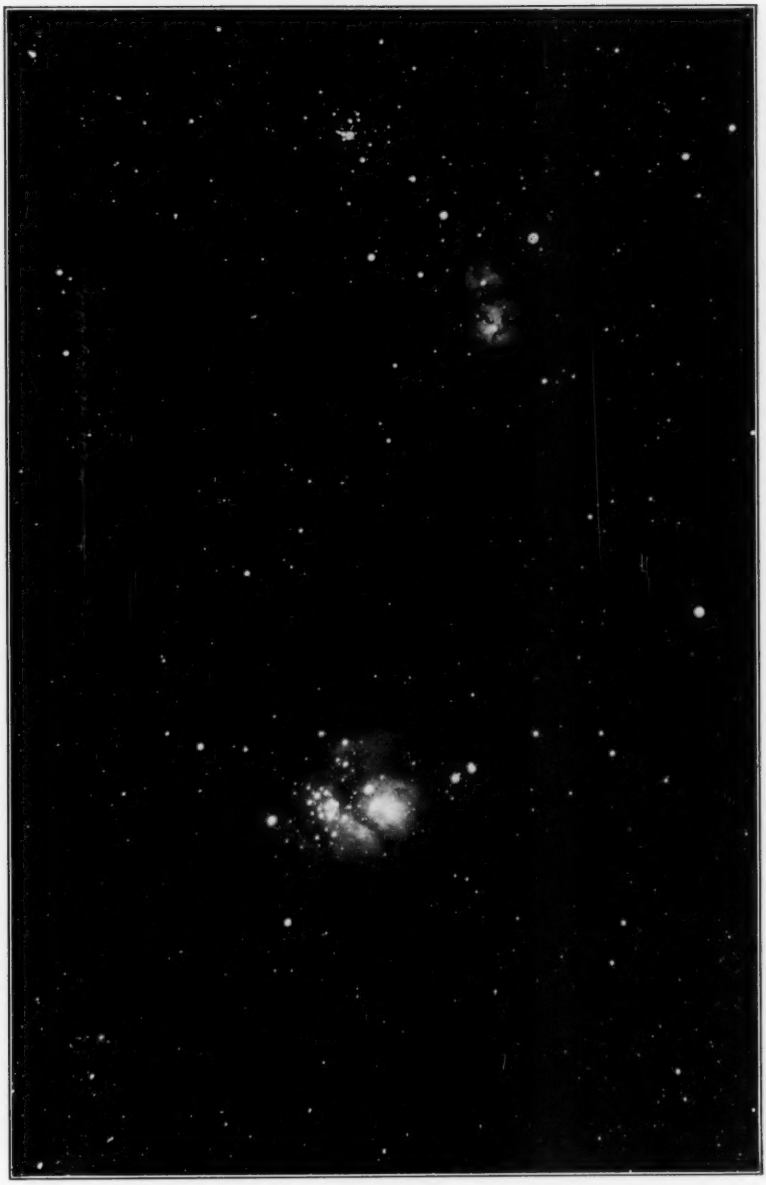

FIGURE 2

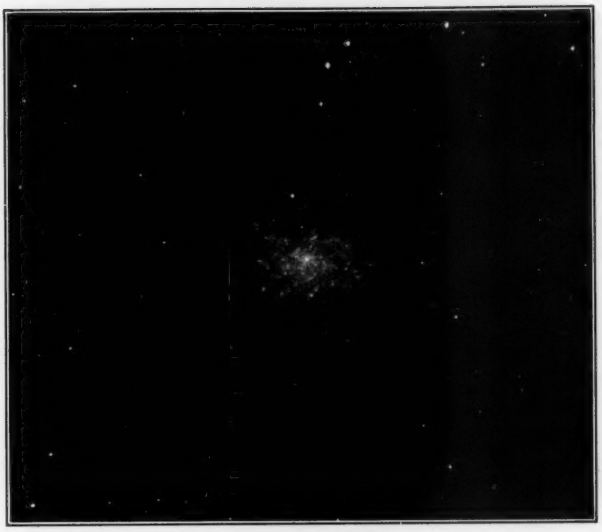

FIGURE 3

FIGURE 4

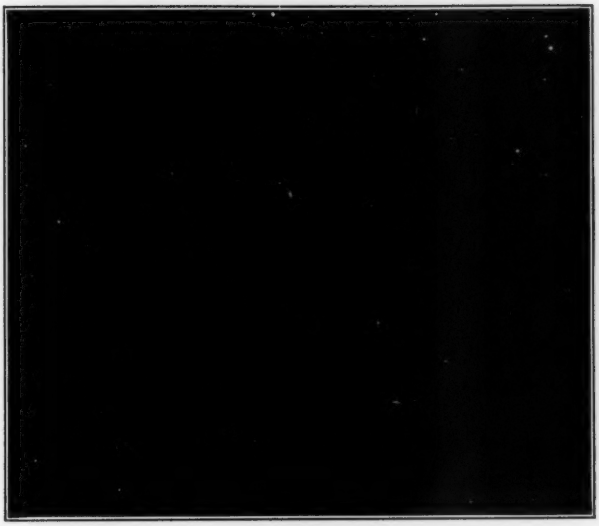

FIGURE 5

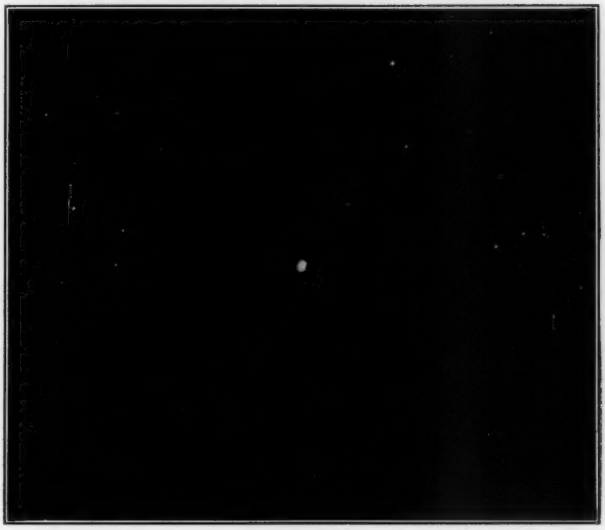

FIGURE 6

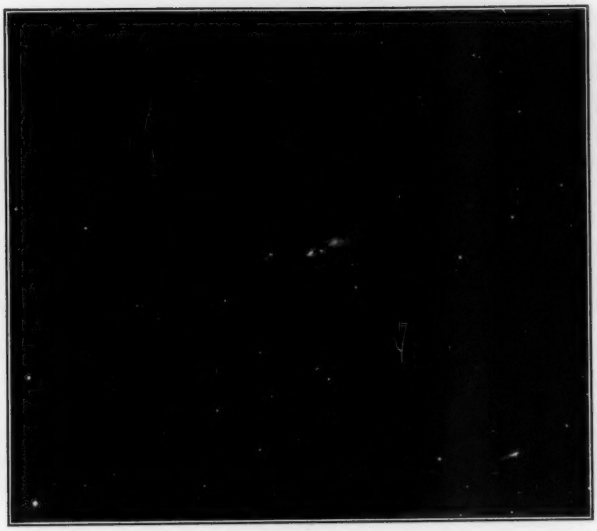

FIGURE 7

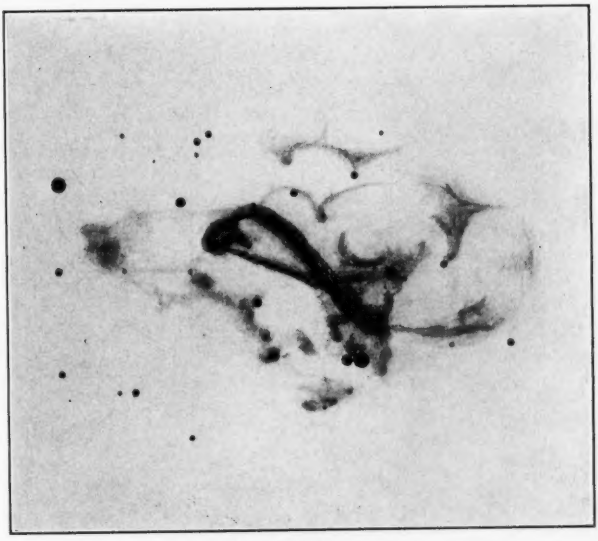

FIGURE 8

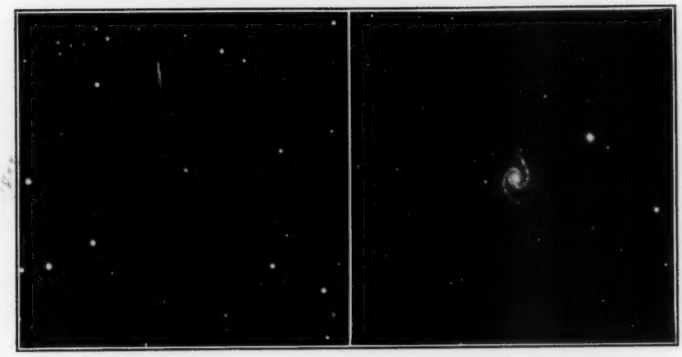

FIGURE 9

FIGURE 10

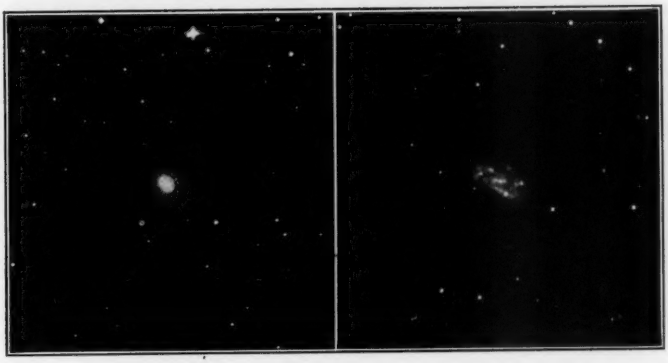

FIGURE 11

FIGURE 12

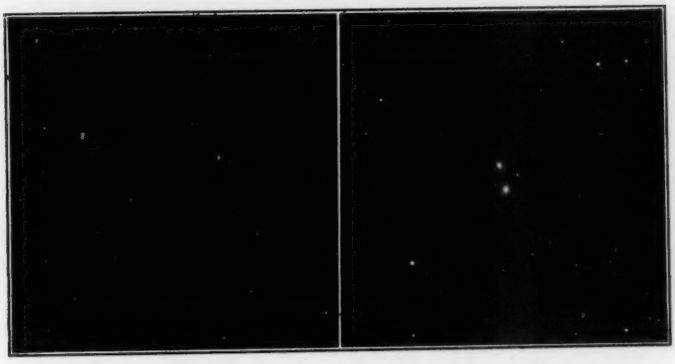

FIGURE 13

FIGURE 14

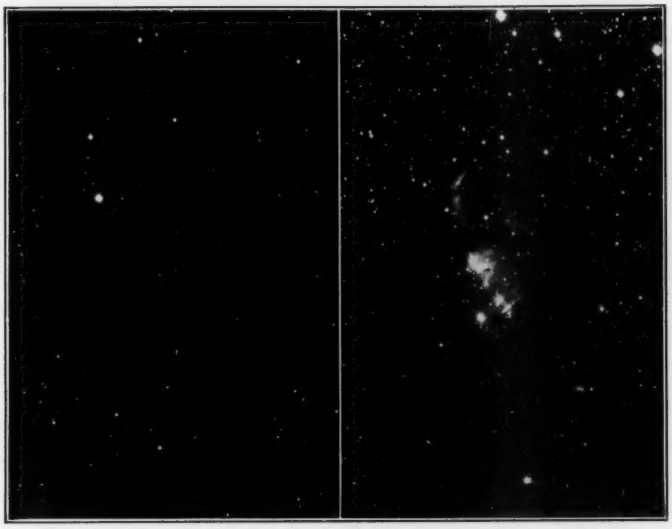

FIGURE 15

FIGURE 16

FIGURE 17

FIGURE 18

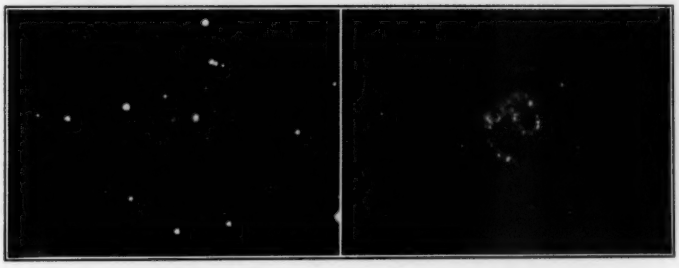

FIGURE 19

FIGURE 20

FIGURE 21

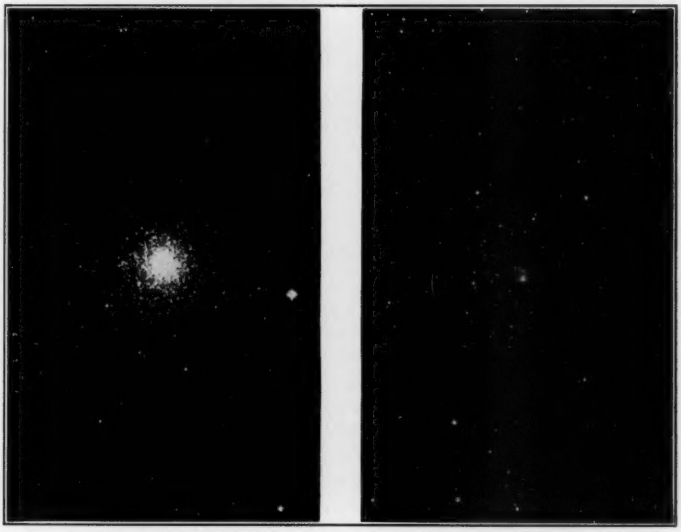

FIGURE 22

FIGURE 23

striking differences between red and blue plates are to be noted, except the sharper contrast on the red plate between light and dark nebulosity along the borders and in the crater-like area, 1.3 cm. in diameter, 1.6 cm. above and to the left of Eta Carinae. Star clusters stand out more sharply on the red plates. The reproduced blue photograph had an exposure of one hour, with the seeing "unsteady and fuzzy at times."

2. The four-hour exposure with the Bruce doublet on a region in Sagittarius ten degrees from the galactic center shows both the strong irregular absorption that marks this interesting section of the Milky Way and two familiar objects: the Lagoon Nebula, Messier 8 (NGC 6523) with its star cluster, and the Trifid Nebula, Messier 20 (NGC 6514). Also, at the center top of the picture is the bright open cluster Messier 21 (NGC 6531). That these two large gaseous nebulae are separated by scarcely more than the diameter of Messier 8 is commonly overlooked. Stars fainter than the eighteenth magnitude appear on the reproduction. The area shown is approximately $2^{\circ}.3$ by $3^{\circ}.4$.

3. The nebular class *Sd* might well be used for NGC 7793 and similar objects of the spiral class that go far beyond the average *Sc* type in openness and lack of central concentration. Spiral arms are not distinct for NGC 7793; for the typical *Sc* spiral Messier 83 in figure 4 they dominate the structure.

A photometric study of NGC 7793 by Shapley and Mohr is published in *Harvard Bulletin* 907 (1938). The object was discovered in 1850 during cometary searches by George P. Bond, working visually with a comet seeker at the Harvard Observatory. A noteworthy feature, shown in figure 3, is the group of outlying patches of irregular nebulosity, especially at the western central edge of the photograph and in the southwestern quadrant. The reality of these nebulous patches is verified by other photographs. They are probably distantly outlying parts of the spiral nebula, although apparently far beyond detectable spiral arms. Since the distance of the spiral is estimated at 810 kpc., the diameters of the patches are of the order of 100 pc. Probably a similar outlying patch near the spiral Messier 101 is the irregular object NGC 5477; but NGC 5477 has a nucleus, whereas many of the nebulosities near NGC 7793 are without central concentration. Exposure 68 minutes.

4. NGC 5236 = Messier 83 is one of the brightest spirals in the sky (see plate II, *Lick Obs. Pub.*, **13,** 42 (1918)). It lies in a region richly populated with faint nebulae, and is within two degrees of the great Centaurus cluster of galaxies (*Harv. Bull.* 874 (1930)). Exposure 75 minutes, with the seeing recorded as "impossible."

5. The spirals NGC 7582–90–99, which probably form a physical system, are much alike in dimensions, inclination and class, but they differ considerably in structural details. Faint spiral arms appear to envelop the main body of NGC 7582; and NGC 7599 has no strong nucleus. Within two degrees of these three are five other equally large and bright spirals, NGC 7496, 7531, 7552, 7632 and IC 5325—all probably members of the group. The reflector plate of two hours exposure, reproduced in figure 5, shows 154 faint nebulae, many of which are retained in the reproduction.

6. The unusual barred spiral NGC 1097 loses much of its fine structure in the reproduction (see also Reynolds, *M. N.*, **85,** 101 (1925)). The large nucleus (burned out in the reproduction) shows a strong rift and a peculiar internal structure that perhaps result chiefly from the distribution of obscuration. Along the swollen or elliptical "bar" and in the spiral arms there are also peculiar obscurations and markings.

The spiral of class *Sa*, 17 mm. to the northwest of the nucleus and apparently within one of the spiral arms, is probably not connected with NGC 1097; its magnitude (on small-scale plates) is approximately 14. Exposure 101 minutes.

7. With a diameter of more than half a degree ($32'.6 \times 4'.4$), NGC 55 probably is exceeded in angular dimensions among the spirals only by the Andromeda Nebula and Messier 33. Since it is considerably more distant than either of these objects, its linear

dimensions also may be outstanding among the galaxies. The object is so peculiar that it cannot easily be classified. Is it, perhaps, a highly resolved spiral without nucleus, nearly on edge; or an equally tilted system of the Magellanic type; or possibly two overlapping systems, similarly inclined, with similar internal structure? The third interpretation, suggested in conversation by Dr. G. Z. Dimitroff, is lent color by the appearance of the object on small-scale long-exposure plates (see inset in figure 7), where it appears to be a double, edge-on spiral, without nuclei and with the components differing perhaps three magnitudes in total brightness. Strong absorption may conceal nuclear regions; but a number of spirals that appear to be devoid of a central nucleus or strong central concentration are now known. It may well be that such objects will need to be recognized as forming a distinct class.

No Cepheid variable stars or novae have as yet been found in NGC 55, but South African plates for the detection of such distance indicators are accumulating. The brightest stars are of the eighteenth magnitude, and we might conclude that the system is of the order of 0.7 mpc. distant with an overall diameter of 7 kpc. Exposure two hours; poor seeing.

8. NGC 5189, near the galactic equator, is a gaseous nebula of such remarkable knotted structure that it is here best represented by a drawing, made by Miss Virginia McKibben from an original reflector plate. No bright star is involved in the nebulosity, but 6′ to the south is the seventh magnitude star H. D. 117694, spectrum B9. In the Henry Draper Catalogue there is no star with a spectrum earlier than B5 within a degree of the nebulosity. The overall dimensions of the nebula are $3'.0 \times 2'.0$. Exposure two hours.

9. The barred spiral NGC 2442–3 very closely resembles NGC 1097 (figure 6, above) in angular dimensions and structure, but it is more than a magnitude fainter and its ellipsoidal and structureless nucleus is decidedly off center. The low latitude, $-21°$, probably accounts for the difference in brightness, and is a measure of the space absorption. The dark absorbing band that follows along the middle of the northern arm is unusually conspicuous. (The large marking across the end of this arm is a plate defect.) Exposure 90 minutes.

10. NGC 1566 is a tenth-magnitude spiral conspicuous for the series of bright clusters, nebulosities or supergiant stars lined up along both spiral arms. Less than one turn from the nucleus the arms suddenly become completely devoid of these condensations. Exposure two hours.

11. NGC 6753 is a face-on spiral; its interesting nuclear structure is not shown clearly in the reproduction. The thin closely wound arms start from the rim of a sharp-edged nearly circular disc, 23″ in diameter, much as with a typical barred spiral, but there is no certain indication of the typical bar. The bright nucleus in the center of the disc is nearly stellar in sharpness. See the description below of figure 13. Exposure one hour; seeing fair.

12. The high latitude, $-41°$, of NGC 1559 probably makes it necessary to conclude that the object is really a galaxy of peculiar form, perhaps an irregular barred spiral. The most central of the twenty nebulous condensations is not the brightest. There is too much regular structure to justify assigning this object to the Magellanic type. When the west side is taken as the top of the picture, the form of the object suggests a giraffe's head. Exposure one hour; seeing unsteady.

13. It is remarkable that two such unusual but similar systems as NGC 6935 and 6937 should be only 4′ apart, and both face-on. In total brightness, in diameter of the central plate or disc and in magnitude of the central nucleus they are almost identical; but NGC 6937 shows distinct spiral arms, and its companion only faintly suggests an external structure of some sort just outside the bright-rimmed plate. Densitometer

tracings verify the appearance in detail, showing for both objects that the rim of the nearly circular plate is brighter than the plate itself, and showing also for NGC 6935 the probable existence of spiral arms. For NGC 6937 there is a suggestion of a bar across the center; probably these "plate spirals" are related to the common barred spirals. The nuclear structure of NGC 6753 (figure 11, above) is similar. An examination of many other nebular plates taken with the Bruce and Metcalf telescopes shows that NGC 4622 and NGC 5055 (Messier 63) may be of this same type, and NGC 4507 and NGC 4750 are somewhat similar. Perrine has described NGC 6935–37 in *Monthly Notices*, **82**, 487 (1922). Exposure one hour.

14. NGC 4782–3 appear on first inspection to be a connected pair of spheroidal nebulae, but the densitometer tracings show that one of the objects (NGC 4782) has a structure suggestive of a class *S0** or *Sa* spiral. The bridge between the two objects may therefore be illusory. Many plates show the apparent connection distinctly. Exposure one hour.

15. The brightest star in the picture of NGC 2736, the "Streak" nebula, is H. D. 77433, spectrum A3. This peculiar streak of nebulosity, 20′ long, appears wedge-shaped, on the original plate, about 3′ wide at the base, with the point of the wedge to the south; but only the bright western boundary of the nebulous area shows clearly in the reproduction. Exposure one hour; seeing poor.

16. The diffuse gaseous nebulosity in Carina, NGC 3581, is on the galactic equator, less than 4° east of the Eta Carinae Nebula. The reproduction satisfactorily brings out the details of bright and dark nebulosity as shown by the original plate, although by increasing the contrast the interesting indistinct obscurations at the top of the picture could be enhanced. Exposure 75 minutes; "at times through thin haze."

17. A series of photographs of varying exposures would be necessary to bring out the intricate details of the bright planetary NGC 3132 = H. D. 87877. It could well be named the "8-burst" planetary from the number of distinct arcs on the boundary of the main disc or shell. The class A star H. D. 87892, magnitude 9.5, is centrally superposed. The object has been studied spectroscopically by the Lick Observatory (*Lick Obs. Pub.*, **13**, 118 (1918)). Exposure one hour.

18. A new object of the Magellanic Cloud type is revealed by the photograph of IC 4662. The next figure also shows an object of this kind, but neither is bright enough to be considered a member of the local group of galaxies. IC 4662 is resolved on the 60-inch plates, but its brightest stars are of about the nineteenth magnitude, with star clusters up to the fifteenth magnitude or brighter. Exposure 99 minutes; seeing fair.

19. NGC 6438, described in Dreyer's catalogue as "pretty bright, round, very gradually brighter in middle," refers only to the spheroidal member of a strange pair—probably a physical double. The other member is of the Magellanic type, unresolved on the 60-inch plates. The moderately high latitude, −27°, much decreases the likelihood that the irregular component is a gaseous nebula, superposed on the field. There is no neighboring high temperature star. The affiliation of these two extreme forms of galaxies reminds one of the analogous association of the giant globular cluster 47 Tucanae and the Small Magellanic Cloud, but that association is a coincidence of direction, since the Small Cloud is perhaps five times the distance of the cluster. Exposure two hours.

20. Two catalogue numbers, NGC 4038 and NGC 4039, have been given to the very peculiar "ring-tail" structure shown in figure 20. The object has been described by Gregory, Perrine and Duncan, and a picture made with the Mount Wilson 100-inch reflector is given in *Mount Wilson Contribution* 256 (1923). The high latitude, +43°, gives assurance that the object belongs to the category of external galaxies. It is reminiscent of the "giraffe's head" in figure 12 above, but is much more like NGC 4027 (not reproduced here). The two are, in fact, nearly identical, and again we note as remark-

able that such odd structures come in pairs; they are separated in the sky by only seven-tenths of a degree, and are of nearly the same magnitude (11.0 and 11.6), angular dimensions, and structural peculiarities. Almost certainly they are physically associated, or have been. (The same must also be true for the "plate spirals" in figure 13.) The objects are one-armed spirals of a sort, with open ring nuclei. At least for NGC 4038–9, a hazy irregular nebulosity, cut by absorbing lanes, surrounds the ring and arm. The Bruce plates clearly show the great extent of two streamers from this hazy enveloping nebulosity, giving an overall diameter of more than a quarter of a degree (*Mt. W. Contr.* 256, 4 (1923); *Harv. Ann.*, **88**, 98 (1934)). The central ring and a part of the arm are outlined by bright stars or stellar groups.

A spectroscopic study of the object will be undertaken by the McDonald Observatory; a photometric analysis will be made at Harvard. Exposure one hour.

21. The globular cluster Omega Centauri = NGC 5139, shown here with a sixty-minute exposure under fairly good conditions of seeing, is unquestionably one of the most remarkable stellar systems. Its total absolute magnitude is comparable to that of the smaller external galaxies, such as the companions to the Andromeda Nebula.

22. NGC 7099 is the globular cluster Messier 30.

23. An open galactic cluster in low latitude and a small bright gaseous nebula together bear the catalogue number NGC 2818. The star cluster is little more than a chance thickening of the galactic star field.

* A class between *E*7 and *Sa*, recently proposed by Hubble.

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## *ON THE DETERMINATION OF THE ORBITAL ELEMENTS OF ECCENTRIC ECLIPSING BINARIES*

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A systematic and elegant procedure was devised[1, 2, 3, 4] by H. N. Russell and H. Shapley, for finding the orbital elements of eclipsing stars from their light curves. In their procedure the fundamental equations for the loss* of light, $\alpha$, during an eclipse in a circular orbit, are

$$\cos^2 i + \sin^2 i \sin^2 \theta = \delta^2 \qquad (1)$$

and

$$\delta = r_1 \{1 + kp(k, \alpha)\}, \qquad (2)$$

where $i$ is the inclination, $\theta$ is the mean anomaly measured from mid-eclipse, $\delta$ is the apparent distance between centers, $r_1$ is the radius of the larger star, $kr_1$ is the radius of the smaller star, the unit of distance is the radius of the relative orbit, and $p(k, \alpha)$ is a known and tabulated function

of $k$ and $\alpha$. If the orbit is eccentric, then equation (1) must be replaced by equation (23) of Russell's[2] paper II; this exact equation

$$r^2\{\cos^2 i + \sin^2 i \cos^2 (v + \omega)\} = \delta^2 \qquad (23)$$

may be written in the equivalent form

$$\{\cos^2 i + \sin^2 i \sin^2 (v + \omega - 90°)\} \frac{(1 - e^2)^2}{(1 + e \cos v)^2} = r_1^2[1 + kp(k, \alpha)]^2. \qquad (23')$$

In the last two equations the unit of distance is the semi-major axis of the orbit of the brighter star relative to the fainter, $r$ is the radius vector, $e$ is the orbital eccentricity, $v$ is the true anomaly, and $\omega$ is the longitude of periastron measured from the ascending node in the direction of motion. The problem that arises in practice is to find a set of elements that, inserted in equation (23′), will reproduce to within the observational accuracy the known, rectified, light curve. Such definitive elements can be obtained in general only by the adjustment of preliminary, approximate, values. By treating each eclipse-curve separately as though the orbit were circular, "circular" elements can be obtained from either or both of them, and Russell[2] gave simple equations for finding, from the "circular" elements, approximate values of the true elements. Russell's equations yield closely approximate elements when $e$ is small; but the equations are correct only through terms of the first degree in $e$, and when $e$ exceeds two or three tenths their accuracy is impaired.

For most of the known eclipsing stars, $e$ is smaller than two tenths; but some eclipsing stars are known for which $e$ considerably exceeds† this limit. Precise orbital elements of such stars are needed in order to investigate their concentrations[6, 7, 8] of density; and it therefore becomes desirable to obtain formulae, closely approximate for large values of $e$, that express the true elements in terms of the "circular" ones. In this note, such formulae are presented. Several alternative forms for them are possible, differing from one another in accuracy and complexity. The more accurate forms are in general the more complicated. It is desirable for the formulae to be simple and easy of application; and since the resulting approximate values of the true orbital elements should probably always be tested and if necessary improved by the exact equation (23′), it is permissible to sacrifice some accuracy in order to gain simplicity. The formulae to be given here are simple; they fit naturally into the procedure of Russell's paper II; they are believed to be so accurate that in many cases no subsequent adjustment will be necessary of the elements that they yield; and they agree as well as they should,‡ to the first degree in $e$, with Russell's equations that they are intended to replace.

Consider the eclipse of the brighter star by the fainter. At the instant of conjunction, $v = 90° - \omega$, and $r = (1 - e^2)/(1 + g)$ where $g = e \sin \omega$. At this instant also, the rate at which $v$ is increasing is $\dot{v} = n(1 + g)^2/(1 - e^2)^{3/2}$ where $n$ is the mean motion. Let us ignore the variations of $r$ and $\dot{v}$ during eclipse. Then if we denote the true anomaly measured from conjunction by $\beta = v + \omega - 90°$, and the mean anomaly measured from mid-eclipse by $\theta'$, we shall have with considerable accuracy that $\beta = \theta'(1 + g)^2/(1 - e^2)^{3/2}$. Now $e$ is in general small unless the stars are widely separated, and then $\beta$ remains small during eclipse. Thus $\sin^2 \beta$ is approximately equal to $\sin^2 \theta'(1 + g)^4/(1 - e^2)^3$, and (23′) may be written in the approximate form

$$\frac{(1 - e^2)^3}{(1 + g)^4} \cos^2 i + \sin^2 i \sin^2 \theta' = r_1^2 \frac{1 - e^2}{(1 + g)^2} \{1 + kp(k, \alpha)\}^2,$$

valid for the eclipse of the brighter star. Since $i$ must be fairly close to 90°, this equation is nearly equivalent to

$$\cos^2 i' + \sin^2 i' \sin^2 \theta' = r_1'^2\{1 + kp(k, \alpha)\}^2, \tag{3}$$

where $(1 + g)^2 \cot i' = (1 - e^2)^{3/2} \cot i$, and $(1 + g)r_1' = r_1(1 - e^2)^{1/2}$. If equation (3) is compared with equations (1) and (2) it is seen to be the same as the exact equation that would hold in a circular orbit of unit radius, having the same period and the same $k$ as the real orbit, but having a radius $r_1'$ for the larger star and an inclination $i'$. In the same way, if $\theta''$ is the mean anomaly measured from the instant of mid-eclipse of the fainter star by the brighter, it can be shown that the light curve during that eclipse must be nearly the same as in a circular orbit having the same period and $k$ but with an inclination $i''$, and a radius $r_1''$ for the larger star, given by

$$(1 - g)^2 \cot i'' = (1 - e^2)^{3/2} \cot i, \text{ and } (1 - g)r_1'' = r_1(1 - e^2)^{1/2}.$$

Preliminary elements may therefore be obtained by following the procedure outlined by Russell,[2] but with the present equations (30′) replacing his equations (30),

| Primary minimum | Secondary minimum |
|---|---|
| $r_1' = r_1 \dfrac{(1 - e^2)^{1/2}}{1 + g}$, | $r_1'' = r_1 \dfrac{(1 - e^2)^{1/2}}{1 - g}$, |
| $\cot i' = \dfrac{(1 - e^2)^{3/2}}{(1 + g)^2} \cot i$, | $\cot i'' = \dfrac{(1 - e^2)^{3/2}}{(1 - g)^2} \cot i$. |

(30′)

Russell's equation (31) may be used as it stands for obtaining the first, rough, approximation to $e \cos \omega$; but it should then be replaced by

$$\frac{h(1-e^2)^{1/2}}{1-g^2} + \tan^{-1}\frac{h}{(1-e^2)^{1/2}} = \frac{\pi}{P}(t_2 - t_1 - \tfrac{1}{2}P), \qquad (31')$$

where $h = e \cos \omega$. Equation (31') is exact[7] for central eclipses, and becomes very accurate** in all cases provided that its left-hand member is increased by the often negligible correction

$$\tfrac{1}{2}h(1-e^2)^{1/2}\cot^2 i\left\{\frac{1}{(1+g)^3 + (1+g)(g+g^2+3h^2)\cot^2 i} + \frac{1}{(1-g)^3 + (1-g)(-g+g^2+3h^2)\cot^2 i}\right\},$$

where the quantity in curly brackets is nearly equal to two. Russell's equations (32) should be replaced by

$$r_1'' = r_1'\frac{1+g}{1-g}; \qquad \cot i'' = \left(\frac{1+g}{1-g}\right)^2 \cot i'. \qquad (32')$$

His equations (33), (34) and (35) are unaltered, and one has still, of course, that

$$\frac{\delta_1}{\delta_2} = \frac{1-g}{1+g}. \qquad (4)$$

As has been mentioned, the above formulae have been obtained by adopting constant values of $\dot{v}$ and of $r$, for each eclipse, equal to their instantaneous values at the moments of conjunction. If the eclipses are wide, it should be somewhat more accurate to use, instead, values averaged over the durations of the eclipses. The equations that result from the averaged values are the same as the equations given above, except that $g$, in equations (30') and (32') only, should be replaced by $g\eta$. With sufficient approximation, $3\eta = 2 + \zeta$, where $\zeta$ is the cosine of the average of $\theta'$ and $\theta''$ at the beginning or the end of eclipse. However, when $e$ is large the eclipses will in general be narrow, $\eta$ will be effectively equal to unity, and the equations as they have been given, without $\eta$, should be sufficiently accurate to yield good preliminary values of the true orbital elements.

As a practical test of the accuracy of the equations of this note in a particular case, a set of true elements was adopted: $r_1 = 0.118$, $r_2 = 0.098$,

cot $i$ = 0.0201, $e$ = 0.506, $\omega$ = 330°. From these a light curve was computed by the exact equation (23′), and from the light curve "circular" elements were obtained: $r_1'$ = 0.1364, cot $i'$ = 0.02312, $r_1''$ = 0.0823, cot $i'$ = 0.00830, $k$ = 0.8305. The formulae (30) of Russell, when applied to $r_1'$ and $r_1''$, yielded for $r_1$ the values 0.109 and 0.110, respectively, of which the average, 0.110, is in error by nearly eight per cent because of the large value of $e$. The same formulae, applied to cot $i'$ and cot $i''$, yielded for cot $i$ the values 0.0154 and 0.0167, respectively, the average, 0.0160, being in error by over twenty per cent. The equations (30′) of the present note, when applied to $r_1'$ and $r_1''$, yielded for $r_1$ the values 0.118 and 0.120, the average, 0.119, being only one per cent in error; and when applied to cot $i'$ and cot $i''$ they yielded for cot $i$ the values 0.0201 and 0.0203, the average, 0.0202, being in error by only one-half of one per cent, or twenty seconds of arc.

*Summary.*—Simple and closely approximate formulae are given, valid for large values of the orbital eccentricity $e$, for deriving preliminary values of the true orbital elements of an eclipsing binary star from the "circular" elements of its eclipses. The formulae are equivalent to Russell's (*Ap. J.*, **36,** 54 (1912)), designed for small values of $e$, when $e$ is small; they are more accurate than Russell's when $e$ is large.

* For the unit of $\alpha$, which depends upon the law of darkening and upon which of the two stars is in front, the reader is referred to papers 1 through 4.

† For one such star, see reference 5, in which it is stated that for H. V. 7498, $e$ exceeds 0.4.

‡ Exactly, if $\eta$ is employed; otherwise, very closely.

** Equation (31′) as it stands gives exactly the time-interval between conjunctions; the correction has been computed from $v$ and from the $\beta$'s that minimize $\delta^2$ for the two eclipses. The value of $\beta$ for the instant of deepest eclipse is obtained from the first and second derivatives of $\delta^2$ with respect to $v$ at the conjunctions. The instants $t_1$ and $t_2$ are those of deepest eclipse.

[1] Russell, *Ap. J.*, **35,** 315 (1912).
[2] Russell, *Ap. J.*, **36,** 54 (1912).
[3] Russell and Shapley, *Ap. J.*, **36,** 239 (1912).
[4] Russell and Shapley, *Ap. J.*, **36,** 385 (1912).
[5] Shapley and Swope, *Bull. Harvard Coll. Obs.*, No. 909, 5 (1938).
[6] Sterne, *M. N.*, **99,** 451 (1939).
[7] Sterne, *M. N.*, **99,** 662 (1939).
[8] Sterne, *M. N.*, **99,** 670 (1939).

# GALACTIC AND EXTRAGALACTIC STUDIES, IV. PHOTOMETRY OF TWO LARGE SOUTHERN CLUSTERS OF GALAXIES

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1. The most conspicuous deviation from uniformity in the space distribution of galaxies is shown by the clustering into large populous groups such as the widespread organization in Virgo and the more compact cluster in Coma at the north galactic pole. Something less than twenty of these rich systems, each containing hundreds of galaxies, have been reported. On the other hand, more than fifty small groups are in our records at present and hundreds are within the range of existing telescopes. They are clusters involving ten to fifty members, frequently very compactly associated and usually in fields of irregular density. The most important of these less populous groups is undoubtedly our own local aggregation, with the galactic system, the Magellanic Clouds, the Andromeda Nebula, the Sculptor and Fornax dwarf galaxies, and a few others as members.

The present communication treats of two systems of the larger type, both of them newly discovered. The significance of the detailed photometric study on Harvard plates, which has recently been completed, lies in the contribution to knowledge of

(*a*) the luminosity curve of galaxies (frequency distribution of total absolute magnitudes), and

(*b*) the mean density of matter in "unexpanded" regions of metagalactic space.

2. General information concerning the two groups is given in table 1. The equatorial and galactic coördinates refer to the centers of the clusters. The areas are given in square degrees. The magnitude limits of the plates, $m_g$, indicate the brightness of the faintest star clearly seen near the plate centers. The plate population refers to the total number of galaxies measured in the central twenty-five square degrees of the plate; the cluster population has been deduced after appropriate correction for the superposed images of the general field.

TABLE 1

| GROUP | POSITION IN 1900 R. A. | DEC. | GALACTIC LONG. | LAT. | CLUSTER AREA | POPULATION | PLATE NUMBER | $m_g$ | PLATE POPULATION |
|---|---|---|---|---|---|---|---|---|---|
| *A* | $1^h\ 3^m.7$ | $-16°\ 10'$ | 116° | −77° | 0.88 | 420 | A 18691 | 19.3 | 3847 |
| *B* | 22 21 .4 | $-49°\ 18'$ | 312° | −56° | 0.44 | 300 | A 20255 | 18.6 | 3479 |

For these two systems, as for nearly all others we have studied, the greater part of the cluster population probably lies below the limits of the available plates. We must content ourselves, therefore, with a partial survey, with a census of only the brighter members. Even the brightest objects are so faint that no safe classification of the individuals is possible. We can only say that among them are objects of the usual types—spheroidal and spiral.

3. *Group A.*—The general field of nebulae on plate A 18691, where the

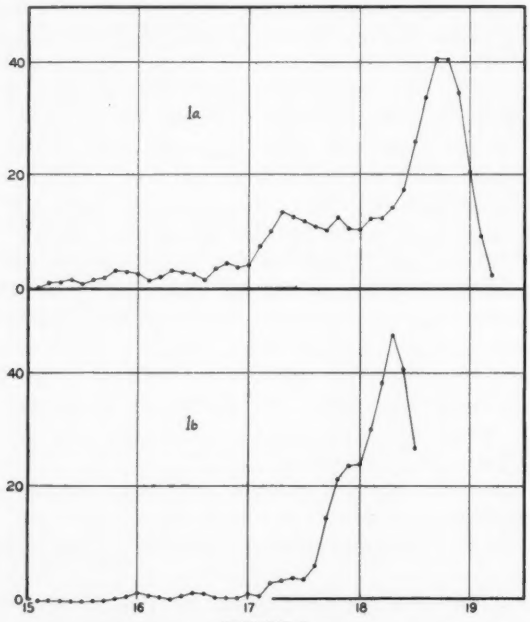


FIGURE 1

Luminosity curves for Group A (above) and Group B. Ordinates are numbers of galaxies; abscissae, apparent photographic magnitudes.

first of the two groups covers 0.88 square degrees, is very unevenly populated. In one particular square degree there are but eighty-seven objects; in an adjacent square degree, three hundred. To remove the field population from the area covered by the cluster is therefore troublesome and uncertain. The simplest and most direct procedure has been followed. First, the magnitudes in a stellar comparison sequence were established by star counts, in connection with the van Rhijn and the Seares and Joyner tables, which relate photographic magnitude to galactic coördinates and

stellar densities. With this sequence the photographic magnitudes of the nearly four thousand nebulae on the plate were twice measured to the nearest tenth of an interval. The frequency distribution of the nebular magnitudes for the eight central square degrees was next determined. To get the average field population for each tenth of a magnitude in an area equal to that covered by the cluster, the factor 0.88/8 was applied to the numbers for each interval. These reduced numbers for the field were then subtracted from the corresponding observed values for the cluster area and the remainders are taken as providing the true luminosity distribution for the cluster members alone.

The size of the corrections applied to the observed numbers in the cluster area is of course a function of the magnitude, and is satisfactorily represented by the relation $N = 10^{0.6(m-16.7)}$, where $N$ is the number of galaxies per 0.88 square degrees to photographic magnitude $m$. The relation is indeed a "uniform density" formula for these particular eight square degrees.

TABLE 2

DATA FOR LUMINOSITY CURVES, CORRECTED FOR FIELD

| MAG. | GROUP *A* | GROUP *B* | MAG. | GROUP *A* | GROUP *B* | MAG. | GROUP *A* | GROUP *B* |
|---|---|---|---|---|---|---|---|---|
| 15.0 | 3.8 | 0.6 | 16.4 | 5.5 | 0.7 | 17.9 | 12.8 | 27.1 |
| 15.0 | 0.0 | −0.2 | 16.5 | 0.1 | 1.6 | 18.0 | 8.7 | 17.2 |
| 15.1 | −0.3 | −0.4 | 16.6 | 1.9 | 1.1 | 18.1 | 9.5 | 27.1 |
| 15.2 | 0.8 | 0.0 | 16.7 | 2.6 | 0.3 | 18.2 | 18.4 | 45.7 |
| 15.3 | 2.7 | −0.3 | 16.8 | 5.9 | −0.6 | 18.3 | 8.9 | 41.6 |
| 15.4 | −0.2 | −0.4 | 16.9 | 4.6 | 1.0 | 18.4 | 15.1 | 52.2 |
| 15.5 | 1.9 | −0.4 | 17.0 | 0.9 | 0.3 | 18.5 | 28.6 | 27.8 |
| 15.6 | 0.8 | −0.2 | 17.1 | 6.9 | 1.4 | 18.6 | 33.8 | |
| 15.7 | 1.8 | −0.1 | 17.2 | 14.2 | −0.1 | 18.7 | 38.7 | |
| 15.8 | 2.9 | −0.4 | 17.3 | 8.9 | 7.5 | 18.8 | 49.2 | |
| 15.9 | 4.6 | 0.9 | 17.4 | 17.1 | 2.4 | 18.9 | 33.7 | |
| 16.0 | 1.4 | 0.7 | 17.5 | 11.8 | 1.7 | 19.0 | 20.8 | |
| 16.1 | 1.7 | 1.8 | 17.6 | 6.6 | 6.5 | 19.1 | 6.8 | |
| 16.2 | 1.0 | −0.4 | 17.7 | 14.4 | 9.8 | 19.2 | −0.1 | |
| 16.3 | 3.1 | −0.3 | 17.8 | 10.0 | 26.6 | | | |

The data for the luminosity curve are given in table 2 and plotted in figure 1*a*, where the points are running means, each representing three-tenths of a magnitude. The curve is somewhat unusual for a cluster of galaxies. The rising branch is over 3.5 magnitudes in length, instead of the usual 2.5 magnitudes, or less. The remote possibility that a cluster of bright objects, magnitude 15 to 17.5, is superposed on a faint cluster, beginning about 17.0, has been considered. The plots in figure 2*a* show, however, that the center of the cluster is essentially identical for bright, intermediate, and faint objects and therefore that a single system with a wide spread in luminosity is the only reasonable hypothesis.

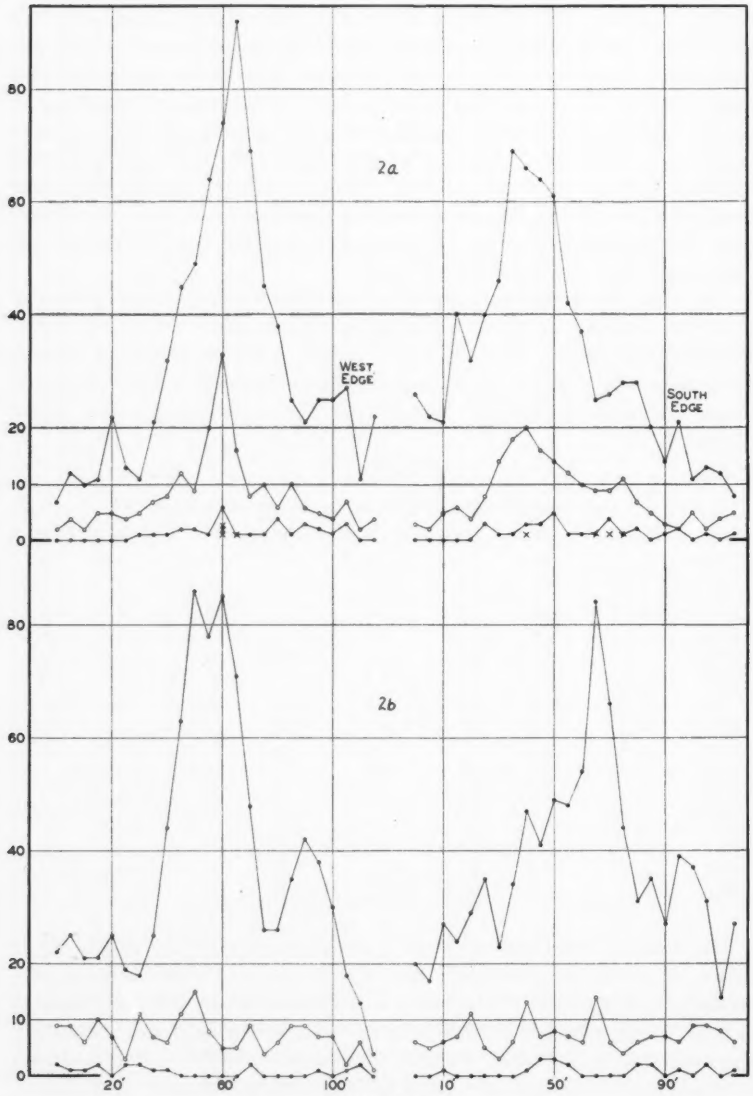


FIGURE 2

Distribution of galaxies in and around Group A (above) and Group B. Ordinates are numbers of objects in strips 5′ wide and 2° long. The plots on the left represent summations for the strips running north and south, beginning at the east side of the four-square-degree areas; the figures on the right give the summations for the strips

The cluster lies in a rich region, and the distribution over the whole plate (thirty square degrees) is irregular. In fact, it is noteworthy that nearly all of the very rich clusters of galaxies are situated in regions of irregular distribution and frequently in regions of very high field density. There is in this fact an indication that a physical connection exists between heavy clustering and non-homogeneity in the field—an intimation that an earlier high space density, perhaps of the order of $10^{-26}$ or $10^{-27}$ g./cc., is dissolving or breaking up, and, in the environs of the cluster, approaching the more normal density of $10^{-29}$ or $10^{-30}$ g./cc. that appears to prevail in intergalactic space. On this hypothesis the cluster which we are now isolating and measuring represents an "unexpanded" region—a remnant or nucleus of a formerly much larger system.

Within the nearly circular area of Group *A* there is greater richness along the north-south axis. This elongation is shown by figure 2*a*, where the distribution of galaxies over four square degrees, centered on the cluster, is represented for objects fainter than photographic magnitude 17.5, and for two brighter intervals. The total numbers of galaxies in strips five minutes of arc wide and two degrees long are shown on the left for strips running north and south, and on the right for the east-west strips. The low values for the south edge of the area are probably due in part to magnitude loss because of distance from the plate center. We should expect, but do not find, a similar loss at the west edge; irregularities in the field population probably compensate for the distance effect. The north-south elongation of the denser portions of Group *A* is shown in figure 2*a*, both for objects fainter than 17.5 and those between 16.0 and 17.5, by the differences in form between north-south and east-west curves.

The positions in the cluster of the four objects with magnitude brighter than 15.5 are indicated by crosses in figure 2*a*. These bright objects (table 3) are probably the giant galaxies of the cluster, with absolute magnitudes not fainter than $-17$, and therefore comparable to the Andromeda Nebula in intrinsic luminosity. The linear dimensions are computed on the assumption that the distance of the group is 29 megaparsecs.

The field nebulae could not be eliminated in making figure 2, but the curves, through indicating the population of the field, provide a check on the method described above for removing field objects before making the luminosity curves in figure 1.

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FIGURE 2 (*Continued*)

running east and west, beginning at the north side. The plotted values have not been smoothed or corrected for the field nebulae. In each of the four sections the distribution of objects fainter than magnitude 17.5 is represented by the upper curve; magnitudes 16.0 to 17.5 inclusive, by the middle curve; and magnitudes brighter than 16.0, by the lower curve. The crosses in figure 2*a* are discussed in the text.

4. *Group B.*—The distribution of galaxies throughout the four square degrees, at the center of which is the second of the two clusters, is shown in figure 3. The positions of objects brighter than 17.5 are indicated by open circles; those of magnitude 17.5 and fainter, by dots. It is clear that there is very little clustering of bright objects, in contrast to the situation in Group *A*. The cluster, according to this diagram, would not be detectable on plates showing objects only to magnitude 17.5. Table 2 and figure 1*b* show, in fact, that when the field galaxies have been removed there remains scarcely an object brighter than magnitude 17. Beginning with magnitude 17.5, however, the luminosity curve rises steeply until the approach to the plate limit interferes with the survey. A total of three hundred cluster members has been measured. (The star-count sequences for Group *B* are based on the van Rhijn tables alone.)

If the distribution of absolute magnitudes in Group *B* is similar to that found at Mount Wilson and Harvard in other rich clusters (for example, the Coma cluster[1]), we should expect the maximum of the luminosity

TABLE 3

GIANT GALAXIES IN GROUP A

| DESIGNATION | CLASS | DIAMETERS ′ × ′ | PHOTOGRAPHIC MAGNITUDE | ABSOLUTE MAGNITUDE | LINEAR DIMENSIONS KPC |
|---|---|---|---|---|---|
| I 78 | S | 2.1 × 0.9 | 14.4 | −17.9 | 18 × 8 |
| I 79 | E1 | 0.7 × 0.7 | 14.9 | −17.4 | 6 × 6 |
| I 82 | Sb? | 0.9 × 0.7 | 14.85 | −17.45 | 8 × 6 |
| 1221 | E3 | 0.5 × 0.4 | 15.4 | −16.9 | 4 × 3 |

curve to be not brighter than photographic magnitude 18, and the total population to be well over a thousand members. Figure 2*b* shows that Group *B* is smaller in angular diameter than Group *A* and that the distribution within its nearly circular outline is not especially elongated, though decidedly irregular, so far as we can judge from the three hundred cluster members above the plate limit. To remove the effects of the field on the cluster's luminosity curve, the same procedure was used as for Group *A*, except that ten square degrees, appropriately selected to avoid differential distance-effects, were studied to determine the probable field membership in the area of 0.44 square degrees occupied by the cluster itself.

It is found that the relation $N = 10^{0.6\,(m\,-\,16.9)}$ satisfactorily represents the frequency of magnitudes for an average field of 0.44 square degree in this galactic latitude and longitude. Reducing the formula to its value for one square degree, we find a space density parameter

$$N_1 = 16.3$$

which closely agrees with the mean value for the whole of the southern galactic hemisphere in high latitudes. In other words, the average population in the vicinity of Group $B$ apparently is normal, whereas for Group $A$ we find $N_1 = 16.55$, a value indicating a density considerably below average, although not beyond the limit of common fluctuations from average density.

5. *Estimate of Distances.*—The high galactic latitude and the richness of the surrounding fields both suggest that little correction to the apparent

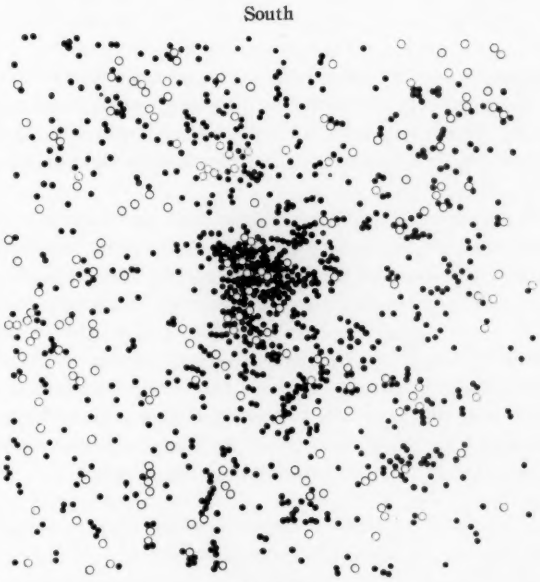


FIGURE 3

Distribution of objects in four square degrees centered on Group B. Objects fainter than magnitude 17.5 are indicated by dots; brighter objects, by open circles. Stars in this field are not plotted.

magnitudes need be made for space absorption. A small correction for the red shift is necessary since the velocity of recession for such distant clusters exceeds ten thousand kilometers a second. Following the method originally used for globular star clusters and later adapted by Hubble to the study of clusters of nebulae, we may estimate the distances of these two groups from the apparent magnitudes of the fifth brightest member or the thirtieth, as well as from the apparent magnitude at the maximum of the luminosity curve. In the following tabulation $\Delta m_{\beta,\lambda}$ is the adopted

correction to the observed apparent magnitudes for space absorption and red shift; $m_5$ is the corrected apparent magnitude of the fifth brightest cluster member; $m - M_1$ is the resulting distance modulus when we adopt, on the basis of Harvard and Mount Wilson studies of the nearer rich clusters, the absolute magnitude $-16.3$ for the fifth brightest object in a rich system.

| GROUP | $\Delta m_{\beta,\lambda}$ | $m_5$ | $m - M_1$ | MAXIMUM MAGNITUDE | $m - M_2$ |
|---|---|---|---|---|---|
| *A* | 0.2 | 15.0 | 31.3 | 18.6: | 32.8 |
| *B* | 0.3 | 16.6 | 32.9 | 18.8+ | 32.9+ |

The maximum of the luminosity curve is uncertainly estimated for Group *A*, and is merely guessed from the shape of the ascending branch for Group *B*. The magnitudes corrected for absorption and red shift are in the next to the last column, and in the last is the resulting distance modulus.

Obviously the distances calculated from this material are only approximate; if they are within twenty per cent of the true values they suffice to give useful information on the luminosities and diameters of the brighter members and an indication of the space density of galaxies in these large systems. It seems appropriate to give only half-weight to the distance modulus derived from the fifth magnitude in Group *A* because of the unusual form of the luminosity curve. Half-weight should also be given to the value estimated from the unobserved maximum of Group *B*. We adopt, therefore, the mean moduli of 32.3 and 32.9 for Group *A* and Group *B*, respectively. The corresponding distances are

Group *A*, 29 megaparsecs
Group *B*, 38 megaparsecs

With the distance as indicated for Group *A*, it appears certain that some of the brightest members of the cluster are comparable in total absolute magnitude with the Andromeda Nebula for which Hubble estimates the brightness at $-17.5$. The values of linear dimensions and absolute magnitudes are given above in table 3. If really a member of the group, one of the objects, *IC* 78, which appears to be a spiral on edge, with a strong nucleus, is fifty per cent larger than the Andromeda Nebula as ordinarily photographed.

In an earlier survey of magnitudes in twenty-five clusters of galaxies,[2] where a few groups were found to be of this very populous type, we had already indicated the presence of a few giant galaxies, some of which were approximately of the luminosity and linear dimensions of the giants here recorded.

With the distances as indicated above, the linear diameters of Group *A* and Group *B*, respectively, are 0.27 mpc. and 0.25 mpc. But it is probable that many of the objects lying further afield are also physical members of these super-systems and the true dimensions, if boundaries can be fixed, exceed a million light years.

We are indebted to Miss Frances W. Wright for making second measures on all the magnitudes and for other assistance with this research.

*Summary.*—(*a*) In the study of nearly eight thousand galaxies on two exceptionally good three-hour plates, made with the Bruce refractor at the Boyden Station, two rich groups have been found and measured. They bear the same relation to the ordinary small group of galaxies as globular clusters bear to galactic clusters, but the rich groups of galaxies are not highly or isometrically centralized.

(*b*) The distances are 29 and 38 megaparsecs for Groups *A* and *B*, respectively, and their diameters exceed two hundred and fifty kiloparsecs.

(*c*) The plates do not reach to the faintest objects in either system, but when appropriate correction is made for field nebulae we count approximately four hundred cluster members in Group *A* and three hundred in Group *B*, and estimate the total populations at approximately a thousand each. The corresponding space densities are probably in excess of $10^{-27}$ g./cc.

(*d*) The luminosity curve deduced for Group *B* is very similar to that found for other rich systems of this sort; but in Group *A* there appears to be a considerable number of unusually bright galaxies which are almost certainly members of the system and not merely superposed field galaxies (figure 1).

(*e*) The giant systems in Group *A* are of both the spiral and spheroidal types. Some of them are comparable with the Andromeda Nebula in luminosity, and one of them, *IC* 78, a spiral on edge, appears to exceed the Andromeda Nebula both in luminosity and in linear dimensions, if it is not by chance a nearer superposed galaxy.

[1] *Mt. W. Contr.* No. 427, 22 (1931); No. 549, 7 (1936); *Harv. Bull.*, **896**, 9 (1934).

[2] These PROCEEDINGS, **19**, 1002 (1933).

# THE DOPPLER EFFECT IN RESONANCE LINES

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The problem of the Doppler broadening of spectral lines consists of two parts, the computation of the absorption coefficient as a function of position in the line and the determination of the distribution of the scattered light over the line. It has generally been supposed in astrophysical applications that the condition of monochromatic radiative equilibrium is present in the formation of resonance lines. That this is not the case, under conditions when Doppler broadening is present, follows from the fact that the projected velocity, and hence the Doppler shift, of an atom is not generally the same along the direction of the scattered ray as it is along the primary ray. The absorption coefficient for combined damping and Doppler broadening is well known and has been used extensively. In the present report we consider the second problem, the distribution of the scattered light over the various parts of a spectral line.

In the absence of Doppler broadening the absorption coefficient is

$$\frac{\pi e^2}{mc} Nf \frac{\gamma}{\pi} \frac{1}{\gamma^2 + (\nu - \nu_0)^2}.$$

Here $N$ is the number of atoms per gram of the gas and $\gamma$ is the natural half breadth.

Let us now consider the scattering into a direction making an angle $\alpha$ with the original ray. Let us choose rectangular coördinates $(u_1, u_2, u_3)$ such that the plane $u_3 = 0$ contains the two rays and the $u_1$ axis makes an angle $\alpha/2$ with each of the two rays. An atom having velocity components $(u_1, u_2, u_3)$ will have a projected velocity along the primary ray

$$u_1 \cos \alpha/2 - u_2 \sin \alpha/2,$$

and along the scattered ray

$$u_1 \cos \alpha/2 + u_2 \sin \alpha/2.$$

A frequency $\nu'$, as referred to the moving atom, corresponds to frequencies $\nu_1$ and $\nu_2$ as seen along the primary and scattered rays, respectively. Their values are as follows:

$$\left.\begin{aligned} \nu_1 &= \nu' + \frac{\nu}{c}(u_1 \cos \alpha/2 - u_2 \sin \alpha/2), \\ \nu_2 &= \nu' + \frac{\nu}{c}(u_1 \cos \alpha/2 + u_2 \sin \alpha/2). \end{aligned}\right\} \quad (1)$$

The distribution of velocities for a kinetic temperature $T$ is given by the expression

$$\left(\frac{Am_1}{2\pi kT}\right)^{3/2} e^{-\frac{Am_1}{2kT}(u_1^2+u_2^2+u_3^2)}\, du_1, du_2, du_3.$$

Here $A$ is the atomic number and $m_1$ is the mass of an atom of unit atomic number.

The energy absorbed per gram from an incident beam of unit intensity by the atoms in the velocity intervals $du_1$, $du_2$ and $du_3$ is

$$\frac{\pi e^2}{mc} Nf \frac{\gamma}{\pi} \frac{1}{\gamma^2 + (\nu' - \nu_0)^2} \left(\frac{Am_1}{2\pi kT}\right)^{3/2} e^{-\frac{Am_1}{2kT}(u_1^2+u_2^2+u_3^2)}\, du_1, du_2, du_3. \quad (2)$$

This energy is scattered into the various directions according to the phase function

$$\frac{3}{16\pi}(1 + \cos^2 \alpha).$$

Let us introduce the following abbreviations:

$$b = \left(\frac{2kT}{Am_1}\right)^{1/2} \frac{\nu_0}{c},$$

$$\kappa_0 = \frac{\pi e^2}{mc} Nf \frac{1}{\sqrt{\pi} b},$$

$$a_1 = \gamma/b,$$

$$a_2 = \gamma/b \sec \alpha/2,$$

$$v_1 = \frac{\nu_1 - \nu_0}{b},$$

$$v_2 = \frac{\nu_2 - \nu_0}{b},$$

$$x = \frac{\nu_0}{cb} u_1.$$

Except for subscripts these symbols have the meanings usually ascribed to them.[1]

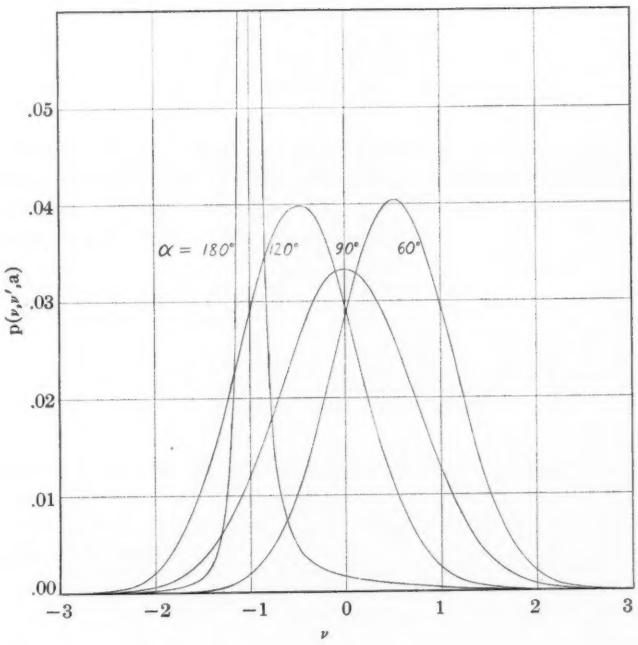
It follows from these relations and from (1) that

$$v_2 = v_1 + \frac{2\nu_0}{bc} u_2 \sin \alpha/2,$$

$$\frac{v_1 + v_2}{2} = \frac{\nu_1 - \nu_0}{b} + \frac{\nu_0}{bc} u_1 \cos \alpha/2.$$

TABLE 1

| $\alpha \backslash v_2$ | −2.5 | −2.0 | −1.5 | −1.0 | −0.5 | 0.0 | +0.5 | 1.0 | 1.5 | 2.0 | 2.5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $a_1 = 0.01$ | $v_1 = 0.0$ | | | | | |
| 60° | 0.0001 | 0.0011 | 0.0020 | 0.0104 | 0.0293 | 0.0399 | 0.0293 | 0.0104 | 0.0020 | 0.0011 | 0.0001 |
| 90° | 0.0001 | 0.0007 | 0.0041 | 0.0118 | 0.0260 | 0.0335 | 0.0260 | 0.0118 | 0.0041 | 0.0007 | 0.0001 |
| 120° | 0.0000 | 0.0002 | 0.0022 | 0.0109 | 0.0288 | 0.0402 | 0.0288 | 0.0109 | 0.0022 | 0.0002 | 0.0000 |
| 180° | 0.0000 | 0.0000 | 0.0001 | 0.0006 | 0.0029 | 1.920 | 0.0029 | 0.0006 | 0.0001 | 0.0000 | 0.0000 |
| | | | | | $a_1 = 0.01$ | $v_1 = 0.5$ | | | | | |
| 60° | 0.0002 | 0.0005 | 0.0007 | 0.0051 | 0.0191 | 0.0377 | 0.0356 | 0.0194 | 0.0052 | 0.0007 | 0.0005 |
| 90° | 0.0001 | 0.0007 | 0.0035 | 0.0124 | 0.0260 | 0.0333 | 0.0261 | 0.0143 | 0.0039 | 0.0007 | 0.0001 |
| 120° | 0.0001 | 0.0008 | 0.0051 | 0.0189 | 0.0367 | 0.0370 | 0.0194 | 0.0054 | 0.0009 | 0.0001 | 0.0000 |
| 180° | 0.0000 | 0.0001 | 0.0004 | 0.0022 | 1.916 | 0.0037 | 0.0010 | 0.0004 | 0.0002 | 0.0001 | 0.0000 |
| | | | | | $a_1 = 0.01$ | $v_1 = 1.0$ | | | | | |
| 60° | 0.0000 | 0.0000 | 0.0002 | 0.0020 | 0.0105 | 0.0286 | 0.0404 | 0.0294 | 0.0103 | 0.0021 | 0.0002 |
| 90° | 0.0001 | 0.0007 | 0.0037 | 0.0129 | 0.0263 | 0.0332 | 0.0258 | 0.0121 | 0.0035 | 0.0006 | 0.0001 |
| 120° | 0.0002 | 0.0021 | 0.0110 | 0.0290 | 0.0398 | 0.0293 | 0.0114 | 0.0025 | 0.0005 | 0.0001 | 0.0000 |
| 180° | 0.0000 | 0.0002 | 0.0017 | 1.893 | 0.0047 | 0.0016 | 0.0009 | 0.0005 | 0.0003 | 0.0001 | 0.0000 |
| | | | | | $a_1 = 0.1$ | $v_1 = 0.0$ | | | | | |
| 60° | 0.0001 | 0.0002 | 0.0022 | 0.0109 | 0.0289 | 0.0398 | 0.0289 | 0.0109 | 0.0022 | 0.0002 | 0.0001 |
| 90° | 0.0001 | 0.0009 | 0.0045 | 0.0128 | 0.0254 | 0.0326 | 0.0254 | 0.0128 | 0.0045 | 0.0009 | 0.0001 |
| 120° | 0.0002 | 0.0007 | 0.0034 | 0.0121 | 0.0281 | 0.0366 | 0.0281 | 0.0121 | 0.0034 | 0.0007 | 0.0002 |
| 180° | 0.0003 | 0.0008 | 0.0021 | 0.0064 | 0.0274 | 0.2120 | 0.0274 | 0.0064 | 0.0021 | 0.0008 | 0.0003 |
| | | | | | $a_1 = 0.1$ | $v_1 = 0.5$ | | | | | |
| 60° | 0.0000 | 0.0001 | 0.0007 | 0.0049 | 0.0183 | 0.0367 | 0.0370 | 0.0203 | 0.0066 | 0.0007 | 0.0001 |
| 90° | 0.0001 | 0.0008 | 0.0036 | 0.0115 | 0.0244 | 0.0315 | 0.0263 | 0.0153 | 0.0050 | 0.0013 | 0.0003 |
| 120° | 0.0002 | 0.0011 | 0.0056 | 0.0177 | 0.0326 | 0.0344 | 0.0210 | 0.0084 | 0.0023 | 0.0007 | 0.0002 |
| 180° | 0.0003 | 0.0010 | 0.0037 | 0.0208 | 0.2060 | 0.0342 | 0.0102 | 0.0043 | 0.0020 | 0.0010 | 0.0004 |
| | | | | | $a_1 = 0.1$ | $v_1 = 1.0$ | | | | | |
| 60° | 0.0000 | 0.0000 | 0.0002 | 0.0018 | 0.0094 | 0.0265 | 0.0392 | 0.0314 | 0.0135 | 0.0031 | 0.0005 |
| 90° | 0.0002 | 0.0006 | 0.0030 | 0.0104 | 0.0222 | 0.0306 | 0.0294 | 0.0157 | 0.0066 | 0.0027 | 0.0005 |
| 120° | 0.0003 | 0.0020 | 0.0093 | 0.0232 | 0.0288 | 0.0292 | 0.0158 | 0.0065 | 0.0027 | 0.0012 | 0.0005 |
| 180° | 0.0009 | 0.0041 | 0.0258 | 0.2392 | 0.0547 | 0.0184 | 0.0089 | 0.0047 | 0.0025 | 0.0013 | 0.0006 |


.05
.04
.03
.02
.01
.00
$p(\nu,\nu',a)$
$\alpha = 180°$
120°
90°
60°
−3
−2
−1
0
1
2
3
$\nu$

The first of these equations shows that for a given initial frequency and phase angle the final frequency is uniquely determined by $u_2$. The total energy scattered into the frequency $\nu_2$ is therefore given by the integration of the contributions of all velocities $u_1$ and $u_3$. Equation (2) gives these contributions since the energy which is absorbed must be emitted in its entirety. Substituting all of our abbreviations and integrating over all values of $u_1$ and $u_3$, we arrive at the following expression for the coefficient of scattering:

$$\frac{3}{16\pi^{1/2}}\frac{1+\cos^2\alpha}{\sin\alpha}\kappa_0 dv_2 e^{-\left(\frac{v_2-v_1}{2}\right)^2\cos^2\alpha/2}\times \frac{a_2}{\pi}\int_{-\infty}^{\infty}\frac{e^{-x^2}dx}{a_2^2+\left(\frac{v_1+v_2}{2}\sec\alpha/2-x\right)^2}. \quad (3)$$

As an alternative representation we may consider the fraction of the energy which, after being absorbed at $\nu_1$ appears at $\nu_2$ in unit interval of frequency and in direction $\alpha$ in unit solid angle. We get this fraction by dividing by the absorption coefficient $k$ and by $d\nu_2$, and we have

$$p(\nu_1,\nu_2;\ \alpha)=\frac{1}{b}\frac{3}{16\pi^{1/2}}\frac{1+\cos^2\alpha}{\sin\alpha}\frac{\kappa_0}{\kappa}e^{-\left(\frac{v_2-v_1}{2}\right)^2\cos^2\alpha/2}\times \frac{a_2}{\pi}\int_{-\infty}^{\infty}\frac{e^{-x^2}dx}{a_2^2+\left(\frac{v_1+v_2}{2}\sec\alpha/2-x\right)^2}. \quad (4)$$

In case $\alpha = 0$, that is, the light is scattered forward, the energy should appear at exactly the same frequency as that at which it was absorbed. This fact also follows from the preceding formulae. Allowing $\alpha$ to approach zero we can verify that

$$p(\nu_1,\nu_2;\ 0)\begin{cases}\longrightarrow 0 & \text{if } \nu_1\neq\nu_2,\\ \longrightarrow \infty & \text{if } \nu_1=\nu_2.\end{cases}$$

In Table 1 we give a number of values of the quantity given in formula (3). In order to illustrate the effects which are involved, the values for $a_1 = 0.01$ and $v_1 = 1$ are also reproduced in the adjoining diagram. It appears from this diagram that the distribution of the scattered light over frequency has maxima which progressively approach, with increasing phase angle, a position which is exactly opposite the primary frequency. For phase angle zero the frequency is, of course, unchanged while for phase angle $\pi$ the shift is a maximum. In the event that the primary frequency is well outside of the core of the line ($v_1 \gg 1$) the situation is different. In this case the Doppler shifts are negligibly small compared with the distance

from the center of the line and we may expect that the scattered light will be distributed closely about the primary frequency. These considerations may be studied directly from our formulae using the known properties of the functions involved therein.

[1] Cf. Hjerting, *Ap. Jour.*, **88**, 508 (1938).

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## *THE THEORY OF THE VISUAL THRESHOLD. I. TIME AND INTENSITY*

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I. In the development of the theory of photic excitation in organisms a place of especial significance has been occupied by the application of the Roscoe-Bunsen Rule. The rule states that for the production of a fixed quantity of photochemical change the product of intensity and exposure time is constant.

Three chief types of evidence have been concerned in testing the validity of this "reciprocity rule" for photic stimulation. In one, exposure times have been determined for minimal response in 50 per cent of individuals at different intensities of illumination.[1] In the second, the relation between intensity and exposure time for the threshold of excitation has been measured in single individuals.[2] Experiments of a third type have involved a modification of the Roscoe-Bunsen Rule, namely, the Talbot-Plateau Law according to which the photosensory effect of a continuous light is equalled by that of light periodically interrupted with sufficiently high frequency if the intensity is increased so that the mean flux is the same.[3] The physical meaning of the data in experiments of these three kinds actually differs in certain interesting ways, however.[4]

II. We are concerned here only with data of the second type. To the extent to which it can be shown that the Reciprocity Rule is obeyed for the visual threshold, the evidence could be taken to support the notion that the sensory effect at the threshold is due to a constant amount of photochemical disturbance.[5] It has thus an important connection with the common doctrine of the constancy of the effects responsible for discriminatory differences, especially since the same considerations have also been applied to differential thresholds $\Delta I = I_2 - I_1$ as a function of exposure-time.[6]

The existing data relevant to this matter are numerous. They are of two main kinds. A large number of series of measurements show the product of threshold intensity ($\Delta I_0$) and exposure time ($t$) to pass through a minimum.[7] Other series show ($\Delta I_0$) $\times$ ($t$) "constant" up to a critical time,[8] beyond which $\Delta I_0$ approaches constancy. No entirely comprehensive survey of this situation seems to have been made. For consistency's sake it would seem desirable to restrict the use of photochemical considerations in the interpretation of visual data to those measurements involving time-intervals so short as may be known to give approximate constancy in the $I \times t$ product under the conditions; but this would depend upon the assumption that $I \times t$ is really a constant when not complicated by observational errors and when not obscured by the effects of a "critical time" for the delivery of excitation.[8] The explanation of the increase of the $I \times t$ product with longer times has been made in terms of the balance of light—and dark—reactions.[5] This does not account for those data in which $I \times t$ passes through a minimum.

The effort has sometimes been to explain the minimum in ($\Delta I_0$) $\times$ ($t$) as due to technical errors in timing, or to ocular movements. These suggestions are not convincing; nor are they really necessary. The condition for a minimum in the product is obviously that the relative rates of change of $\Delta I_0$ and of $t$ should be numerically equal but of opposite sign—namely, at the point of 45° slope in the curve of log $\Delta I_0$ vs. log $t$. If no such point is included in the range of $\Delta I_0$ and $t$, which is partly determined by the area of the test-patch used and the wave-length composition of the light, or if the time-intervals are too widely spaced, no minimum will be apparent. A theoretical interpretation is required which will embrace the full range of the $\Delta I_0$, $t$ data and which will permit the physical evaluation of the rôle of other variables, for example, of retinal area.

The situation is, of course, qualitatively identical in certain essential particulars with that presented by the phenomena of electrical excitation in nerve, as regards the approach to constant quantity of electricity for excitation as a limit for short times, and in the exhibition of an energy minimum.[9] It is also seen in the deviation from the Reciprocity Rule for blackening of a photographic plate.[10] Into these parallels we need not now go, beyond pointing out that they can probably all be brought under the same kind of explanation.[4]

III. Reasons of several kinds have been advanced[11] for taking $1/I$, where $I$ is the exciting intensity, as the measure of excitability. For threshold excitability we have $1/\Delta I_0$. The threshold intensity acts upon an assemblage of units of which the momentary capacities for excitation form some kind of a frequency-distribution of $dk$, where $k$ is a velocity constant. The dependence of $1/I$ upon the temperature in responses to visual flicker at constant flash frequency shows[11] that $1/I$ behaves as

if governed by the activation of a catalytically controlled intrinsic reaction velocity, to which $1/I$ is directly proportional. The units constituting a homogeneous set exhibit this velocity in statistical distribution, but with the same *kind* of control in each. Under these conditions a velocity constant has the meaning of a reciprocal time. The excitability at the point of threshold response, with continuous exposure, is measured by $1/\Delta I_0$. In the critical excitation of flicker, flashes of intensity $I_c$ are presented repetitively, a large number of times, for single durations $= t = 1/F$, where $F$ is the flash frequency. The critical $I_c$ has therefore the meaning of a $\Delta I_0$; the conditions of its recognition as a distinct flash are different from those imposed when a single, non-repeated flash is used,[12] but the nature of $I_c$ as essentially the equivalent of a $\Delta I_0$ is sufficiently clear.[13] Excitation is the result of the production of impulses by units exhibiting a frequency distribution of instantaneous thresholds, and thus of $d(1/I)$; the number of impulses to be obtained over a finite time from a unit briefly remaining in any given frequency class will be a declining function of intensity above its threshold intensity (accommodation), and consequently the frequency distribution of these impulses will be in terms of $-I.d(1/I)$, and thus of $d \log I$.[14] But $1/I$ exhibits[11] the properties of $k$, proportional to $1/t$ if the temperature is constant, and hence we must expect that $d \log I \equiv cd \log t$. The peculiar quantity signified by the logarithm of a *time* is thus understandable in terms of the proportionality of *time* and the reciprocal of a *velocity constant*. Consequently we expect to find $1/\Delta I_0$ measured by the summation of the impulses provided in the integral of the frequency distribution of $d \log t$.

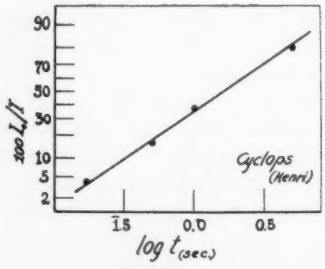


FIGURE 1

Reciprocal threshold intensity for phototropic effect (ultra-violet light) as a percentage of the reciprocal of a minimum $I_0$, as a function of log exposure time, for *Cyclops*.[19] The ordinate scale is that of a probability integral.

The form of this function is suspected to be a normal probability integral.[4] The reasons, briefly, are: (1) the individual elements are nerve impulses; (2) the incidence of an impulse is ruled by probability considerations in a given excitable unit;[15] these elements are quantal, and their effects add to produce a total effect; moreover, the relations of effect to temperature show that, in nerve,[16] and as for *log I* in visual responses,[11] $\sigma_{\log t}$ can be independent of mean *log t* and is not determined by it. Consequently all the assumptions basic to the derivation of a Gaussian curve[17] appear to be specifically justified in this particular case.

IV. The kinds of experimental quantitative modification to which the 3 parameters of this particular function can be put[18] provide the deciding

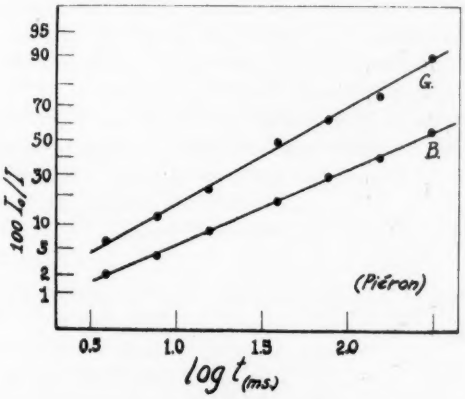


FIGURE 2

Representative data for green ($G$) and for blue ($B$) light, from Piéron,[20] showing that the relations between $1/\Delta I_0$ and log $t$ are satisfactorily rectified in a probability grid.

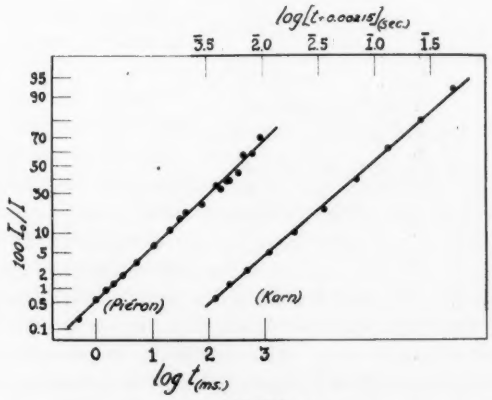


FIGURE 3

Data from Piéron[20] and from Karn,[21] on a probability grid (see text).

test of its propriety. Its application to a number of really homologous instances superficially of quite different sorts is considered at some length

in another place,[4] and has been referred to briefly in an earlier note.[16] The purpose here is to illustrate the application to the complete range of some representative sets of measurements, including several for which the $I \times t$ product goes through a minimum. When the complete range can be accounted for, there is no necessity to invoke a "critical" intermediate time. The illustrations are taken from data of considerable range which there is reason to regard as adequately homogeneous.

In figure 1 there are given data from Henri and Henri[19] for the phototropic threshold of *Cyclops* (ultra-violet light). Figures 2 and 3 give several series of data from Piéron[7] and one from Karn.[20] Numerous other series of available data have been treated in the same way. The data from Karn illustrate one consequence of the fact that the binocular threshold, used in this series, is fundamentally lower than the mean monocular threshold;[21] a given intensity therefore behaves with binocular presentation as if it were acting for a longer time than when presented monocularly—hence the time measured behaves as if in reality somewhat longer.

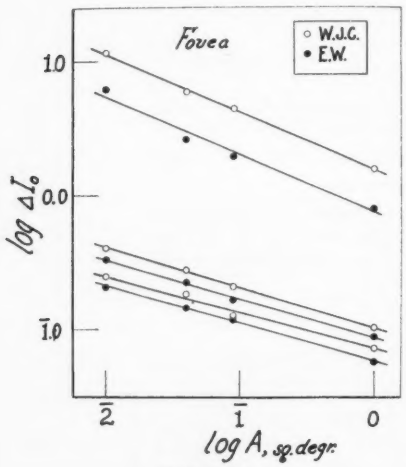


FIGURE 4

Measurements of threshold intensity as a function of area, within the fovea, for two different observers, at three different exposure times (cf., figure 5).

V. It is instructive to consider the way in which the *I-t* function is modified when the retinal area illuminated is changed. It is clear that if in a particular region of the retina the area of the test patch is enlarged, $\sigma'_{\log t}$ should remain the same so long as the area concerned is really homogeneous, although the maximum value of $1/\Delta I_0$ must increase and the abscissa of the inflection point must decrease. If, however, the area is sufficiently enlarged so that factors making for *interaction* become implicated, and consequently there is increased variability of performance in the individual elements, then $\sigma'_{\log t}$ must *increase*. Systematic application of this test has been made in a number of regions of the retina. Results for the fovea are given in figures 4 and 5. They illustrate a significant procedure for the measurement of the extent of retinal area, in different locations, which is critical for the initiation of interaction effects.

The correlation of such critical areas with known or identifiable structural conditions, not necessarily in the retina, presents a number of significant possibilities.

In figure 4 it is apparent that $\Delta I_0$ is a declining power function of the area of the test patch,[22] and that the exponent is a decreasing function of exposure time. The same measurements are given in figure 5 upon a probability grid. They show that when the centrally fixated area approaches 1 sq. degree, interaction effects of the sort already specified make their appearance. The systematic examination of this matter will be considered elsewhere.

VI. *Summary.*—The complete range of data relating the visual intensity threshold to the exposure time can be quantitatively accounted

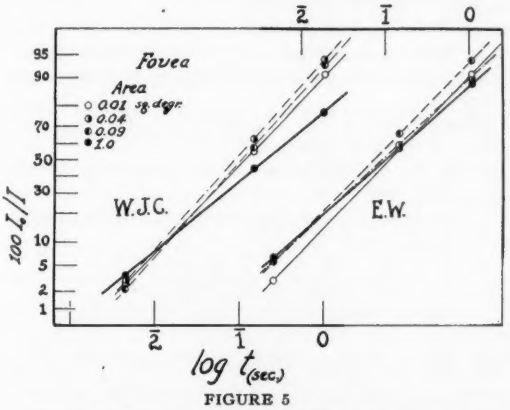


FIGURE 5

The data of figure 4 on a probability grid; see text.

for, with homogeneous measurements, in terms of the theoretical deduction that the reciprocal of the threshold intensity, $1/\Delta I_0$, gives a probability integral in terms of $\log t$. It is unnecessary to suppose that the reciprocity rule has any reasonable application to such measurements. It cannot be deduced from such data either that the sensory effect for threshold occurrence is in any sense a constant, or has anything to do with a constant amount of photochemical change.

Certain properties of the parameters of the probability integral are commented upon, particularly in relation to the area of the retinal image. It is indicated that there arise some testable deductions concerning "interaction."

[1] Blaauw, A. H., *Rec. trav. bot. néerl.*, **5**, 209 (1909); Loeb, J., *Forced Movements, Tropisms, and Animal Conduct*, Lippincott, Philadelphia and London, 209 pp. (1918).

[2] Hecht, S., *Jour. Gen. Physiol.*, **2**, 229, 337 (1919–1920); Piéron, H., *Compt. rend. acad. sci.*, **170**, 525, 1203 (1920).

[3] Cf. Loeb, J., *Forced Movements, Tropisms, and Animal Conduct*, Lippincott, Philadelphia and London, 209 pp. (1918); Hecht, S., and Wolf, E., *Jour. Gen. Physiol.*, **15**, 369 (1931–1932); Gilmer, T. E., *Jour. Opt. Soc. Amer.*, **27**, 386 (1937).

[4] Crozier, W. J., "Theory of the Visual Threshold" (to be published elsewhere).

[5] Hecht, S., Chap. 14 in: *A Handbook of General Experimental Psychology*, pp. 704–828, Worcester, Clark Univ. Press (1934).

[6] Graham, C. H., and Kemp, E. H., *Jour. Gen. Physiol.*, **21**, 635 (1937–1938).

[7] Piéron, H., *Ann. Physiol.*, **15**, 116 (1939).

[8] Graham, C. H., and Margaria, R., *Amer. Jour. Physiol.*, **113**, 299 (1935).

[9] Cf. Hill, A. V., *Proc. Roy. Soc.* (Lond.), **B 119**, 305, 440 (1936).

[10] Cf. Krohn, E., *Jahrb. Phot.*, **28**, 6, etc. (1914).

[11] Cf. *Jour. Gen. Physiol.*, **22**, 311, 487, 795 (1938–1939); **23**, 143; in press (1939–1940); and *Proc. Nat. Acad. Sci.*, **25**, 78 (1939).

[12] Cf. *Jour. Gen. Physiol.*, **19**, 503 (1935–1936); **20**, 393 (1936–1937).

[13] Crozier, W. J., and Holway, A. H., *Proc. Nat. Acad. Sci.*, **23**, 23 (1937); **24**, 130 (1938); *J. Gen. Physiol.*, **23**, 101 (1939–1940).

[14] The frequent utility of a logarithmic transformation for "normalizing" a distribution has long been known and employed in various connections; but this has been done merely by way of the *assumption* that thresholds, for example, are normally distributed in terms of log $I$.

[15] Pécher, Ch., *Compt. rend. soc. biol.*, **122**, 87 (1936); **124**, 839 (1937).

[16] *Proc. Nat. Acad. Sci.*, **23**, 71 (1937).

[17] Cf. Whittaker, E. T., and Robinson, G., *The Calculus of Observations*, 2nd ed. Blackie and Son, Ltd., London (1926).

[18] Crozier, W. J., and Wolf, E., *Jour. Gen. Physiol.*, **23** (1939–1940) (in press); *Proc. Nat. Acad. Sci.*, **26**, 60–67 (1940).

[19] Henri, V. et Mme., *Compt. rend. soc. biol.*, **72**, 992 (1912).

[20] Karn, H. W., *Jour. Gen. Psychol.*, **14**, 360 (1936).

[21] Crozier, W. J., and Holway, A. H., *Jour. Gen. Physiol.*, **22**, 341 (1938–1939); **23**, 101 (1939–1940).

[22] Crozier, W. J., Holway, A. H., and Wolf, E., to be published in detail elsewhere.

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## *TEMPERATURE AND THE CRITICAL INTENSITY FOR RESPONSE TO VISUAL FLICKER. IV. ON THE INVARIANCE OF CRITICAL THERMAL INCREMENTS, AND THE THEORY OF THE RESPONSE CONTOUR*

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Communicated December 14, 1939

1. Experimental evidence discussed in earlier publications has been held to demonstrate certain invariant properties of the flicker-response contour. This contour is defined by the measured relation of flash-frequency $F$ to flash-intensity $I$ critical for response of various animals to visual flicker. The contour, for a specified animal, at a fixed temperature,

and with a given proportion of light-time in the flash-cycle of a given form, is a recoverable function in repeated tests.[1] It is properly described as a band with margins $F \pm \sigma_F$ and $I \pm \sigma_I$, enclosing the region of functional dependence within which homogeneous determinations of the interrelationship of $F$ and $I$ will be found to occur with a given probability.[2]

$F$ is fixed at various levels (or $I$), and critical values of $I$ (or reciprocally of $F$) are experimentally determined for single individuals[3] or for members of a demonstrably homogeneous population,[4] by means of a uniform and widely applicable technique.[5] In cases uncomplicated by the visual duplexity evidenced with most vertebrates,[6] and in an arthropod[7] with opic surfaces sufficiently flat so that mechanical conditions of photic reception do not introduce distortion of the performance contour,[8] the curve relating mean $I$ to $F$ (or mean $F$ to $I$) is efficiently and precisely described by a probability integral in log $I$.[6,7] This formulation provides an efficient[9] and justifiable[10] procedure for the analytical dissection of the duplex response contour of typical vertebrates into two parts,[11] each with a physically distinguishable basis.[10] It also provides a rationalization of the asymetrical curve obtained with most arthropods.[8] The use of a logarithmic probability integral is also supported by the fact[12] that the three parameters of this function are empirically modified by different factors in ways concordant with the general ideas leading to its application.[12]

2. In the derivation of the logarithmic probability integral for the $F$-log $I_m$ curve, and for dynamically similar instances of very diverse character involving the performance of biological systems,[13] use has been made of the idea in the case of photic excitation that *excitability* is properly measured by the reciprocal of the critically exciting intensity $(1/I)$.[13] It has been shown that when the temperature of the organism is altered the $F$-log $I$ curve is not changed in shape, or in the maximum value of $F$ to which (with fixed light-time cycle-fraction) the animal will respond.[14] The curves merely move toward higher intensities as the temperature is made lower.[14] The magnitude of the shift, as a function of temperature, is characteristic of the kind of animal.[15] The direction and the size of the shift require the interpretation that $1/I$ for a fixed level of effect $(F)$ behaves as if controlled by catalytically governed reaction velocities common to all the neutral elements in the population concerned in the determination of the response.[13,15]

A deduction of this kind may be in a significant way justified if it can be shown that the measure of temperature-dependence is not quantitatively modified when certain other variables of the situation are experimentally made to have different values. From this standpoint the properties of the $F$-log $I$ contour are of peculiar interest, in 2 distinct respects. These have to do with $(a)$ the theory of the logarithmic probability integral for the relation between $F$ and $I$, and $(b)$ the conception of

the meaning of quantitatively specific temperature-dependence in biological systems in general.

3. The theory of the basis for the descriptive utility and predictive value of the logarithmic probability integral derives from the general proposition that $d(1/I)$, where $I$ is the critical intensity for response to visual flicker, is frequency-distributed in a certain manner, but that $-kI \cdot d(1/I)$ gives a frequency distribution of the sensory effects produced.[13] If $1/I$ is governed by the velocities of intrinsic chemical events determining the excitability of the elements concerned in the manifestation of the index response, then $1/I_m$ for a homogeneous population of such elements, with a fixed magnitude of responsive discrimination, should be rectilinearly proportional to the exponential of $-\mu/RT$, where $R$ is the gas constant, $T$ = Kelvin temperature and $\mu$ = apparent energy of activation *per* mole of controlling substance (i.e., the *temperature characteristic*[16]). That $\mu$ is independent of the shape of the $F$-log $I$ contour, although dependent on the nature of the animal tested[17] (and thus on its specifically relevant chemical organization[18]), has been amply demonstrated. These facts are clearly confirmatory of the general proposition. It is also required to show, however, that if the form and position of the $F$-log $I$ contour can be modified by some other means than change of temperature, $\mu$ should still be the same provided the primary excitabilities have not been modified (but only the frequencies with which the excitable units contribute to the determination of the end result).

This test is easily made by utilizing the changes produced in the $F$-log $I$ curve when the light-time fraction in the flash-cycle is altered. These changes are non-specific as to direction and form, although specific in amount.[12] When the percentage light-time ($t_L$) is reduced, at constant temperature, the curve rises to a higher maximum $F$, its abscissa of inflection is lowered, both being in rectilinear proportion to the percentage dark-time; the value of $\sigma_{\log I}$ with $F_{\max.} = 100$ *per cent* is not a function of $t_L/t_D$.[12] Consequently we must predict that at any flash-frequency the value of $\mu$ for $1/I$ must be the same with different proportions of light time to dark time, since the latter influences $k$ but not $1/I$ in the expression $-kI \cdot d(1/I)$.

This test has for several reasons been made with turtles of the form *Pseudemys ssp.* The response contour for these animals with purely cone retinas is simple, but the Arrhenius plot of $1/I_m$ exhibits a break at 29.5°.[19] Between 12° and 30° $\mu$ is quite high (26,500 cal.). The results are summarized in figure 1 for $t_L$ = 10 *per cent*, 50 *per cent* and 90 *per cent* of the flash cycle, at $F$ = 25/*sec.* It is apparent that although the $F$-log $I$ contour is altered in the ways already described, $\mu$ = *ca.* 12,400 above 29.5° and $\mu$ = 26,500 from 12° to 29.5° describes the temperature dependence of $1/I$ without reference to the magnitude of $t_L/t_D$.

The reasons for the manner in which change of $t_L/t_D$ alters the $F$-log $I$ curve have already been discussed.[20] It is necessary to suppose that

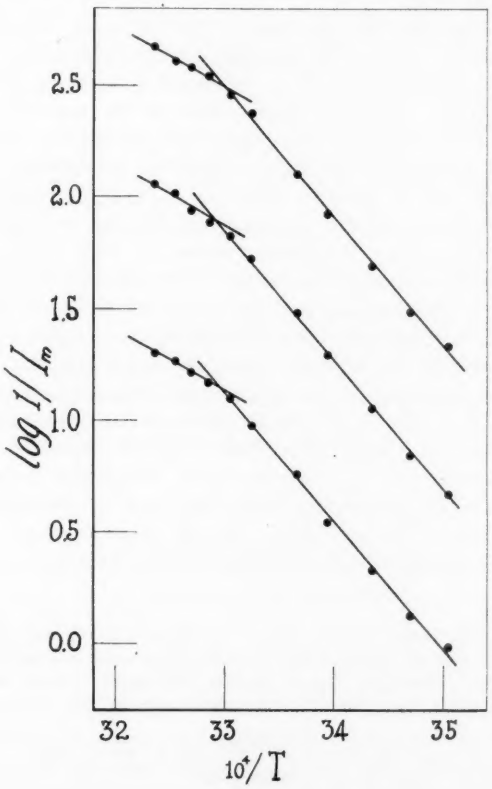


FIGURE 1

Values of log $1/I_m$ critical for response to visual flicker in the dark-adapted turtle *Pseudemys*, as a function of temperature; 1 flash-frequency was used ($F$ = 25) at each of three values of the light-time fraction, 10 *per cent*, 50 *per cent* and 90 *per cent*. Each plotted entry is the mean of 30 determinations. The critical increments characteristic for $1/I_m$ are independent of the alteration in the $F$-log $I$ curves induced by changing the light-time fraction, as shown by the fact that the slopes of the lines on this graph are invariant. These slopes give $\mu$ = 12,400 above 30° and 26,500 below.

with prolongation of dark-time each flash has a greater chance to excite because more elements are likely to be non-refractory; hence the total

number of elements potentially usable over a finite time is enlarged, and thus $f_{max.}$; but the excitability of each element remains the same, and $\sigma'_{\log I}$ is not affected, nor $\mu$.

4. The conception that for many vital processes the form and the magnitude of the dependence on temperature indicate control through activation of a particular catalyst[21] implies that the value of the temperature characteristic should be independent of the constant-temperature magnitude of the velocity concerned. In the present instances $1/I_m$ measures the velocity of processes determining excitability. By choices of $F$ its value can be made to vary over a range of 1:250,000 without change of the slopes of the $\mu$ plots.[22] In the data of figure 1 $1/I_m$ is changed by a factor of 23 without altering $\mu$. These properties demonstrate the important invariant nature of the temperature characteristics when the chemical organization of the system has not been modified.

5. *Summary.*—When the light-time fraction in the flash-cycle is altered it is found that the maximum to which the flicker-response contour rises is directly proportional to the percentage dark-time; the abscissa of inflection of the $F$-log $I_m$ curve decreases in the same proportion, but $\sigma'_{\log I}$ is unchanged. For a given flash-frequency, however, the temperature characteristic of $1/I_m$ with the turtle *Pseudemys* is quantitatively independent of the percentage dark-time, and of the flash-frequency. This variance of $\mu$ has significance for the theory of photic excitability, and for the derivation of the probability integral relating $F$ to log $I$.

[1] Cf. Crozier, W. J., and Wolf, E., *Jour. Gen. Physiol.*, **22**, 463, 487, 795 (1938–1939), etc.; and a more complete account of the present experiments, to be published elsewhere.

[2] Crozier, W. J., *Jour. Gen. Physiol.*, **19**, 503 (1935–1936); Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Ibid.*, **20**, 211, 363 (1936–1937); **21**, 203 (1937–1938); **22**, 311 (1938–1939).

[3] *Jour. Gen. Physiol.*, **21**, 203 (1937–1938); **22**, 311 (1938–1939).

[4] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **20**, 211, 363 (1936–1937); **21**, 17 (1937–1938); Crozier, W. J., and Wolf, E., *Ibid.*, **23**, 1 (1939–1940).

[5] Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **19**, 495 (1934–1935); Crozier, W. J., Wolf, G., and Zerrahn-Wolf, G., *Ibid.*, **20**, 211 (1935–1936).

[6] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **22**, 311 (1938–1939); Crozier, W. J., and Wolf, E., *Ibid.*, **22**, 555 (1938–1939).

[7] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen Physiol.*, **22**, 451 (1938–1939).

[8] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **22**, 451 (1938–1939); Crozier, W. J., and Wolf, E., *Ibid.*, **23**, 1 (1939–1940); *Biol. Bull.*, **77**, 126 (1939).

[9] Crozier, W. J., *Proc. Nat. Acad. Sci.*, **23**, 71 (1937); Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **21**, 17, 203, 313 (1936–1937), etc.

[10] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Proc. Nat. Acad. Sci.*, **23**, 516, 542 (1937); *Jour. Gen. Physiol.*, **21**, 17 (1937–1938); Crozier, W. J., and Wolf, E., *Ibid.*, **22**, 463 (1938–1939); *Proc. Nat. Acad. Sci.*, **25**, 176 (1939).

[11] Cf.,[9] and Crozier, W. J., and Wolf, E., *Jour. Gen. Physiol.*, **23**, 229 (Nov. 1939).

[12] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **20**, 393, 411 (1936–1937); **21**, 223, 313, 463 (1937–1938).

[13] Cf. Crozier, W. J., *Proc. Nat. Acad. Sci.*, **26**, 54–60 (1940).

[14] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Proc. Nat. Acad. Sci.*, **24**, 216 (1938); Crozier, W. J., *Ibid.*, **25**, 78 (1939); Crozier, W. J., and Wolf, E., *Ibid.*, **25**, 171, 176 (1939); *Jour. Gen. Physiol.*, **22**, 487, 795 (1938–1939); **23** (Nov. 1939) (in press).

[15] Cf. *Jour. Gen. Physiol.*, **22**, 487 (1938–1939), etc.

[16] Crozier, W. J., *Jour. Gen. Physiol.*, **7**, 123 (1924–1925); *Proc. Nat. Acad. Sci.*, **10**, 461 (1924).

[17] Crozier, W. J., and Wolf, E., *Proc. Nat. Acad. Sci.*, **25**, 171 (1939); *Jour. Gen. Physiol.*, **23** (Nov. 1939) (in press).

[18] Data on the frequency of breathing movements in two teleost genera and their hybrids, to be discussed elsewhere.

[19] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Proc. Nat. Acad. Sci.*, **24**, 125, 538 (1938); *Jour. Gen. Physiol.*, **22**, 311 (1938–1939).

[20] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **20**, 363 (1936–1937); **21**, 313 (1937–1938).

[21] Cf. Crozier, W. J., *Jour. Gen. Physiol.*, **7**, 189 (1924–1925); **9**, 531 (1925–1926); Hadidian, Z., and Hoagland, H., *Ibid.*, **23**, 81 (1939–1940).

[22] Crozier, W. J., and Wolf, E., *Jour. Gen. Physiol.*, **22**, 487, 795 (1939–1940).

[23] We are under obligation to Mrs. E. Wolf for assistance in the experiments. The more complete account of the work, to be given elsewhere, will include consideration of the variation of $1/I$ within and between individuals.

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## *ON SPINAL SHOCK*

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Communicated November 22, 1939

High reflex excitability and high extensor tone have been observed in the hind legs of cats after the recovery of an isolated caudal part of the spinal cord from certain periods of asphyxia (van Harreveld and Marmont[1]). Since the increased reflex excitability remained in a number of animals for the rest of their lives (up to three weeks), it was concluded that this was caused by a release of the spinal reflexes from a spinal inhibitory mechanism, which in the normal animal depresses them. It was assumed that this inhibitory mechanism was more sensitive to asphyxia than the excitatory structures and that by certain periods of asphyxia the inhibitory mechanism can be eliminated more or less exclusively.

The reflex excitability of the isolated normal spinal cord thus seems to depend on an equilibrium between the functions of excitatory and inhibitory structures. The more active the inhibitory structures, the more the reflex excitability will be depressed, eventually to total areflexia.

Spinal shock, a state of diminished reflex excitability or even of areflexia, which is pronounced only in the primates, might be due to such a dominance of an inhibitory mechanism in the spinal cord. The present experiments were undertaken to see whether, as would be predicted from the above, it is possible to curtail spinal shock by asphyxiating the cord. The monkey, *Pithecus rhesus*, in which Hinsey and Markee[2] recently investigated the spontaneous recovery from shock, was used.

In nine monkeys the spinal cord was severed by a ligature round the dura at Th. 9-Th. 10, thus isolating the caudal part of the spinal cord and dural cavity. Directly after finishing the operation, 10 to 20 minutes after the ligation of the cord, the pressure in the isolated part of the dural cavity was raised above the blood pressure by forcing into it through a canula, physiological solution under a pressure of 24–25 cm. mercury. In this way the blood was prevented from entering the vessels of the cord, for periods between 15 and 30 minutes. After this the reflexes of the hind limbs were examined frequently.

After this procedure a large number of reflexes have been observed often of high, sometimes even of extreme sensitivity. In the following discussion of the results all times are reckoned from the ligation of the cord. In all the experiments brisk tendon reflexes (knee- and ankle-jerks) have developed within a few hours. In many experiments tone was observed in the extensor muscles, sometimes of considerable height, developing within an hour; it has even been possible to record an appreciable stretch reflex from the gastrocnemius group after 4 hours. Skin reflexes appeared in most animals. Movements of the toes elicited by stimulation of the sole (plantar response) were observed after 2 to 3 hours. The flexor reflex in the hind leg and reflex contractions of the tail appeared in many animals after periods ranging from a few hours to 24 hours. The tendon reflexes and tone returned in most animals only temporarily, disappearing after having been manifest for periods between a few hours and 48 hours. In two animals, however, the tendon reflexes remained for life (6 days in both cases). The skin reflexes once developed remained in most cases for the rest of the period of observation (3 to 10 days). In some animals they were of an extreme sensitivity during that entire period.

Hinsey and Markee in a recent paper reported the period of absence of a number of reflexes after transection of the cord in 7 monkeys (*Pithecus rhesus*). They found that the knee-jerk returned after 1 to 20 days (average 7 days). In some cases no ankle-jerk was ever observed, in others this reflex returned after 11 to 62 days. The plantar response was seen after 1 to 20 days (average 6 days) and the flexor reflex after 4 to 102 days (average 27 days). After spontaneous recovery from shock the spinal reflexes are at the beginning very small and it is usually weeks until they reach an appreciable height (Fulton and Sherrington[3]).

Since, as we have shown, quite high reflex activity is often observed beginning a few hours after combined transection and asphyxiation of the cord, there can hardly be any doubt that asphyxia can curtail spinal shock. This return of reflex activity of the isolated and asphyxiated caudal part of the cord as described above is a strong support for the conception of spinal shock as a dominance of an inhibiting structure in the spinal cord itself.

It must be assumed that the reflex activity of the normal animal depends on a continuous depressing influence of the higher centers on the inhibitory mechanism in the spinal cord. The spinal shock following transection of the cord must be considered as a release of that spinal inhibitory mechanism from this depressing higher control, resulting in a diminution and eventual abolition of reflex excitability.

Acknowledgment is gratefully made for assistance from the Neurological Fund of the California Institute of Technology.

[1] van Harreveld, A., and G. Marmont, *Jour. Neurophysiol.*, **2**, 101–111 (1939).
[2] Hinsey, J. C., and J. E. Markee, *Jour. Comp. Neurol.*, **69**, 471–485 (1939).
[3] Fulton, J. F., and C. S. Sherrington, *Jour. Physiol.*, **75**, 17–22 (1932).

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## *PHYSIOLOGY OF DEVELOPMENT OF THE FEATHER. IV. THE DIURNAL CURVE OF GROWTH IN BROWN LEGHORN FOWL*

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### I. INTRODUCTION

Evidences of daily periodicity of functions in fowl are abundant; in this paper we add to them a series of measurements demonstrating that the rate of growth of regenerating feathers is not constant during a 24-hour period, but exhibits considerable fluctuations characterized especially by a very low rate during part of the night. The physiological causes and the morphological consequences of this phenomenon will be discussed after presentation of the data.

Rates of growth during the entire period of regeneration of feathers have been determined several times (cf. Juhn and Gustavson, '30; Juhn, Faulkner and Gustavson, '31; and Lillie, '40). In all these cases the measurements were not less than 24 hours apart; but an analysis of the diurnal distribution of 24-hour increments has not hitherto been attempted.

Owing to limitations of the methods of measuring, it was decided that intervals of less than six hours would be impractical. Accordingly, a first

series of measurements of the growth in six-hour intervals in a continuous 24-hour period was made from the base of twelve o'clock. This series was then repeated at a later date. These measurements showed a very marked decline in growth-rate in the period from midnight to six A. M. The measurements did not, however, necessarily determine very closely the time of lowest or highest rates. Accordingly, two other sets of six-hour increments were prepared using nine o'clock as base. Comparison of the results from the twelve o'clock base and the nine o'clock base enables a closer estimation of the time of minimum growth in a 24-hour period.

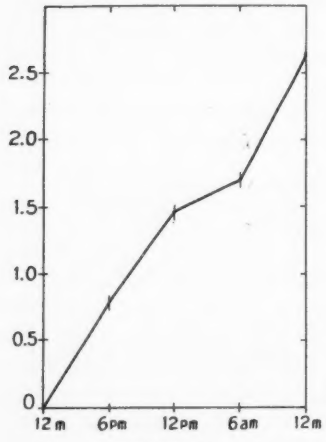


FIGURE 1

Breast feathers. From data of table 1. The grand average of six-hour increments of the three birds plotted. Based on 12:00 o'clock. Ordinates = millimeters of growth; abscissae = time of day.

## II. THE DATA

1. *Six-Hour Increments Based on Twelve O'Clock.*—Ten actively regenerating feathers of the same age in a small area of the breast of each of three Brown Leghorn capons were isolated by removing adjacent feathers; each feather was identified by number and individual records were kept. On the 25th day of regeneration (March 18–19, 1939) measurements were made of the length of each feather at six-hour intervals beginning at noon and terminating at noon of the next day. The increment in length of each feather during each six-hour period was determined from these measurements (table 1). The increments of the individual feathers, 12:00 noon to 6:00 P. M., 6:00 P. M. to 12:00 midnight, 12:00 midnight to 6:00 A. M., 6:00 A. M. to 12:00 noon, were then averaged for each period; the grand average of these increments is plotted in figure 1.

These measurements were then repeated on the same feathers on the 28th day of regeneration (table 2), and similarly averaged. The first and second sets of measurements did not differ significantly.

Determinations of six-hour increments in the growth of saddle feathers (posterior region) were made on the same birds in an exactly similar manner on the 25th day of regeneration (April 18–19, 1939) and again on the 28th day of regeneration (tables 3 and 4). As in the case of the breast, ten feathers identified by number, with individual records for each feather, were used in each bird. Both sets of determinations agreed very closely.

TABLE 1[1]

TWELVE O'CLOCK BASIS. MARCH 18–19, 1939. BREAST FEATHERS BROWN LEGHORN CAPONS. TWENTY-FIFTH DAY OF REGENERATION

| | | 1 12 NOON | 2 6 P. M. | INC. | 3 12 P. M. | INC. | 4 6 A. M. | INC. | 5 12 NOON | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon 148 | 1 | 37.9 | 38.2 | 0.3 | 39.7 | 1.5 | 39.7 | 0.0 | 40.0 | 0.3 |
| | 2 | 37.8 | 37.9 | 0.1 | 38.9 | 1.0 | 39.2 | 0.3 | 39.6 | 0.4 |
| | 3 | 36.5 | 37.1 | 0.6 | 37.1 | 0.0 | 37.8 | 0.7 | 39.2 | 1.4 |
| | 4 | 34.7 | 36.0 | 1.3 | 36.1 | 0.1 | 36.1 | 0.0 | 36.9 | 0.8 |
| | 5 | 35.1 | 35.6 | 0.5 | 36.5 | 0.9 | 37.6 | 1.1 | 37.7 | 0.1 |
| | 6 | 35.0 | 35.6 | 0.6 | 36.5 | 0.9 | 36.8 | 0.3 | 37.6 | 0.8 |
| | 7 | 36.7 | 37.2 | 0.5 | 38.6 | 1.4 | 39.2 | 0.6 | 39.8 | 0.6 |
| | 8 | 36.6 | 36.5 | −0.1* | 37.0 | 0.5 | 37.5 | 0.5 | 38.8 | 1.3 |
| | 9 | 35.6 | 36.1 | 0.5 | 36.9 | 0.8 | 37.3 | 0.4 | 38.4 | 1.1 |
| | 10 | 35.5 | 36.1 | 0.6 | 37.0 | 0.9 | 37.1 | 0.1 | 38.4 | 1.3 |
| | Average | 36.14 | 36.63 | 0.49 | 37.43 | 0.8 | 37.83 | 0.40 | 38.64 | 0.81 |
| | Total increase in 24 hours: | | | 2.50 | | | | | | |
| Capon 171 | 1 | 27.7 | 29.1 | 1.4 | 29.2 | 0.1 | 29.7 | 0.5 | 31.1 | 1.4 |
| | 2 | 29.2 | 29.5 | 0.3 | 30.5 | 1.0 | 31.2 | 0.7 | 33.0 | 1.8 |
| | 3 | 25.3 | 26.3 | 1.0 | 26.6 | 0.3 | 26.6 | 0.0 | 28.3 | 1.7 |
| | 4 | 26.5 | 27.0 | 0.5 | 27.6 | 0.6 | 27.9 | 0.3 | 29.6 | 1.7 |
| | 5 | 33.7 | 34.3 | 0.6 | 34.6 | 0.3 | 34.6 | 0.0 | 36.4 | 1.8 |
| | 6 | 30.1 | 31.2 | 1.1 | 31.9 | 0.7 | 32.0 | 0.1 | 32.5 | 0.5 |
| | 7 | 30.5 | 31.8 | 1.3 | 32.5 | 0.7 | 32.6 | 0.1 | 33.4 | 0.8 |
| | 8 | 30.1 | 30.6 | 0.5 | 31.5 | 0.9 | 31.5 | 0.0 | 32.6 | 1.1 |
| | 9 | 29.6 | 30.2 | 0.6 | 31.0 | 0.8 | 31.4 | 0.4 | 32.2 | 0.8 |
| | 10 | 29.6 | 30.8 | 1.2 | 31.3 | 0.5 | 31.5 | 0.2 | 32.2 | 0.7 |
| | Average | 29.23 | 30.08 | 0.85 | 30.67 | 0.59 | 30.9 | 0.23 | 32.13 | 1.23 |
| | Total increase in 24 hours: | | | 2.90 | | | | | | |
| Capon 139 | 1 | 34.6 | 36.6 | 2.0 | 37.1 | 0.5 | 37.1 | 0.0 | 36.9 | −0.2* |
| | 2 | 33.6 | 34.8 | 1.2 | 36.2 | 1.4 | 36.2 | 0.0 | 36.9 | 0.7 |
| | 3 | 29.2 | 29.3 | 0.1 | 29.9 | 0.6 | 29.9 | 0.0 | 31.5 | 1.6 |
| | 4 | 34.1 | 34.9 | 0.8 | 35.5 | 0.6 | 35.5 | 0.0 | 36.9 | 1.4 |
| | 5 | 32.4 | 34.4 | 2.0 | 34.6 | 0.2 | 34.7 | 0.1 | 35.4 | 0.7 |
| | 6 | 33.2 | 34.8 | 1.6 | 35.0 | 0.2 | 35.1 | 0.1 | 36.3 | 1.2 |
| | 7 | 31.5 | 32.3 | 0.8 | 32.3 | 0.0 | 32.5 | 0.2 | 33.2 | 0.7 |
| | 8 | 33.6 | 35.0 | 1.4 | 35.3 | 0.3 | 35.6 | 0.3 | 36.5 | 0.9 |
| | 9 | 29.6 | 29.6 | 0.0 | 31.4 | 1.8 | 31.4 | 0.0 | 31.5 | 0.1 |
| | 10 | 26.5 | 27.2 | 0.7 | 27.6 | 0.4 | 27.9 | 0.3 | 28.6 | 0.7 |
| | Average | 31.83 | 32.89 | 1.06 | 34.49 | 0.60 | 33.59 | 0.10 | 34.37 | 0.78 |
| | Total increase in 24 hours: | | | 2.54 | | | | | | |
| GRAND AVERAGE | | 32.40 | 33.20 | 0.80 | 33.86 | 0.66 | 34.10 | 0.24 | 35.04 | 0.94 |
| AVERAGE TOTAL INCREASE IN 24 HOURS: | | | | 2.64 | | | | | | |

* Probably due to error.

[1] Tables 1 to 8 give all the original measurements for determination of six-hour increments throughout one day, on which the paper is based, together with the averages for

each bird and the averages of all three together. Columns 1, 2, 3, 4, 5 give the actual measurements in millimeters for the individual feathers. The intervening columns give the increments (Inc.) for the six-hour periods ended in the preceding column. The last horizontal line (grand average) gives the averages of all feathers for each column; the increments in this line are the ones used in the graphs.

TABLE 2

TWELVE O'CLOCK BASIS. SECOND SERIES OF MEASUREMENTS OF THE SAME FEATHERS AS IN TABLE 1. TWENTY-EIGHTH DAY OF REGENERATION

| | | 1 12 NOON | 2 6 P. M. | INC. | 3 12 P. M. | INC. | 4 6 A. M. | INC. | 5 12 NOON | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon 148 | 1 | 47.6 | 48.0 | 0.4 | 49.0 | 1.0 | 49.0 | 0.0 | 50.7 | 1.7 |
| | 2 | 47.8 | 48.5 | 0.7 | 48.9 | 0.4 | 49.1 | 0.2 | 50.4 | 1.3 |
| | 3 | 46.0 | 46.6 | 0.6 | 47.6 | 1.0 | 48.3 | 0.7 | 49.0 | 0.7 |
| | 4 | 45.2 | 45.6 | 0.4 | 46.8 | 1.2 | 47.2 | 0.4 | 48.2 | 1.0 |
| | 5 | 44.4 | 45.2 | 0.8 | 46.0 | 0.8 | 46.4 | 0.4 | 47.4 | 1.0 |
| | 6 | 44.4 | 45.2 | 0.8 | 46.2 | 1.0 | 46.4 | 0.2 | 47.3 | 0.9 |
| | 7 | 46.9 | 48.0 | 1.1 | 48.7 | 0.7 | 49.1 | 0.4 | 49.5 | 0.4 |
| | 8 | 45.9 | 46.8 | 0.9 | 47.0 | 0.2 | 47.5 | 0.5 | 48.4 | 0.9 |
| | 9 | 45.5 | 46.4 | 0.9 | 46.7 | 0.3 | 46.7 | 0.0 | 47.8 | 1.1 |
| | 10 | 45.9 | 46.7 | 0.8 | 47.0 | 0.3 | 47.4 | 0.4 | 48.6 | 1.2 |
| Average | | 45.96 | 46.70 | 0.74 | 47.39 | 0.69 | 47.71 | 0.32 | 48.73 | 1.02 |
| Total increase in 24 hours: | | | | 2.77 | | | | | | |
| Capon 171 | 1 | 37.9 | 38.7 | 0.8 | 39.4 | 0.7 | 39.4 | 0.0 | 40.2 | 0.8 |
| | 2 | 39.4 | 40.1 | 0.7 | 40.9 | 0.8 | 40.9 | 0.0 | 42.0 | 1.1 |
| | 3 | 35.1 | 36.2 | 1.1 | 36.6 | 0.4 | 37.0 | 0.4 | 38.1 | 1.1 |
| | 4 | 35.9 | 36.9 | 1.0 | 37.1 | 0.2 | 37.1 | 0.0 | 38.5 | 1.4 |
| | 5 | 43.5 | 44.5 | 1.0 | 45.1 | 0.6 | 45.6 | 0.5 | 46.1 | 0.5 |
| | 6 | 39.0 | 39.4 | 0.4 | 39.9 | 0.5 | 40.1 | 0.2 | 40.8 | 0.7 |
| | 7 | 39.3 | 39.6 | 0.3 | 40.4 | 0.8 | 40.4 | 0.0 | 41.2 | 0.8 |
| | 8 | 37.6 | 38.7 | 1.1 | 38.9 | 0.2 | 38.9 | 0.0 | 39.5 | 0.6 |
| | 9 | 37.0 | 37.7 | 0.7 | 38.2 | 0.5 | 38.2 | 0.0 | 38.6 | 0.4 |
| | 10 | 38.6 | 38.7 | 0.1 | 40.0 | 1.3 | 40.2 | 0.2 | 40.4 | 0.2 |
| Average | | 38.33 | 39.05 | 0.72 | 39.65 | 0.60 | 39.78 | 0.13 | 40.54 | 0.76 |
| Total increase in 24 hours: | | | | 2.21 | | | | | | |
| Capon 139 | 1 | 44.8 | 45.4 | 0.6 | 46.9 | 1.5 | 46.9 | 0.0 | 47.7 | 0.8 |
| | 2 | 44.4 | 45.4 | 1.0 | 45.9 | 0.5 | 45.9 | 0.0 | 46.6 | 0.7 |
| | 3 | 38.2 | 39.2 | 1.0 | 40.1 | 0.9 | 40.5 | 0.4 | 41.6 | 1.1 |
| | 4 | 44.6 | 45.3 | 0.7 | 46.0 | 0.7 | 46.0 | 0.0 | 47.0 | 1.0 |
| | 5 | 43.0 | 43.6 | 0.6 | 44.3 | 0.7 | 44.5 | 0.2 | 45.0 | 0.5 |
| | 6 | 43.4 | 44.3 | 0.9 | 45.0 | 0.7 | 45.5 | 0.5 | 46.2 | 0.7 |
| | 7 | 41.3 | 42.0 | 0.7 | 42.4 | 0.4 | 42.8 | 0.4 | 43.3 | 0.5 |
| | 8 | 43.8 | 44.3 | 0.5 | 45.0 | 0.7 | 45.2 | 0.2 | 46.1 | 0.9 |
| | 9 | 38.0 | 39.4 | 1.4 | 40.0 | 0.6 | 40.2 | 0.2 | 40.6 | 0.4 |
| | 10 | 34.8 | 36.0 | 1.2 | 37.0 | 1.0 | 37.0 | 0.0 | 37.4 | 0.4 |
| Average | | 41.63 | 42.49 | 0.86 | 43.26 | 0.77 | 43.45 | 0.19 | 44.15 | 0.70 |
| Total increase in 24 hours: | | | | 2.52 | | | | | | |
| GRAND AVERAGE | | 41.97 | 42.74 | 0.77 | 43.43 | 0.69 | 43.64 | 0.21 | 44.47 | 0.83 |

AVERAGE TOTAL INCREASE IN 24 HOURS: 2.50

The grand average of the increments in the first set of measurements is plotted in figure 2.

TABLE 3

TWELVE O'CLOCK BASIS. APRIL 18–19, 1939. SADDLE FEATHERS BROWN LEGHORN CAPONS. TWENTY-FIFTH DAY OF REGENERATION

| | | 1 12 NOON | 2 6 P. M. | INC. | 3 12 P. M. | INC. | 4 6 A. M. | INC. | 5 12 NOON | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon 148 | 1 | 27.4 | 27.9 | 0.5 | 28.8 | 0.9 | 28.9 | 0.1 | 29.9 | 1.0 |
| | 2 | 26.0 | 26.8 | 0.8 | 27.6 | 0.8 | 27.7 | 0.1 | 28.1 | 0.4 |
| | 3 | 26.4 | 26.7 | 0.3 | 27.6 | 0.9 | 27.6 | 0.0 | 28.5 | 0.9 |
| | 4 | 27.4 | 28.2 | 0.8 | 28.3 | 0.1 | 28.4 | 0.1 | 30.0 | 1.6 |
| | 5 | 24.1 | 24.3 | 0.2 | 24.7 | 0.4 | 24.7 | 0.0 | 26.2 | 1.5 |
| | 6 | 25.2 | 25.7 | 0.5 | 26.5 | 0.8 | 27.0 | 0.5 | 27.3 | 0.3 |
| | 7 | 25.3 | 25.7 | 0.4 | 26.5 | 0.8 | 26.6 | 0.1 | 27.5 | 0.9 |
| | 8 | 26.5 | 27.0 | 0.5 | 27.2 | 0.2 | 27.2 | 0.0 | 27.8 | 0.6 |
| | 9 | 25.5 | 25.9 | 0.4 | 26.7 | 0.8 | 27.0 | 0.3 | 27.7 | 0.7 |
| | 10 | 30.2 | 30.9 | 0.7 | 31.6 | 0.7 | 31.7 | 0.1 | 32.6 | 0.9 |
| | Average | 26.40 | 26.91 | 0.51 | 27.55 | 0.64 | 27.68 | 0.13 | 28.56 | 0.88 |
| | Total increase in 24 hours: | | | 2.16 | | | | | | |
| Capon 171 | 1 | 27.9 | 28.2 | 0.3 | 29.2 | 1.0 | 30.0 | 0.8 | 30.5 | 0.5 |
| | 2 | 32.7 | 33.7 | 1.0 | 33.9 | 0.2 | 34.0 | 0.1 | 35.4 | 1.4 |
| | 3 | 28.0 | 28.9 | 0.9 | 29.3 | 0.4 | 29.4 | 0.1 | 30.2 | 0.8 |
| | 4 | 26.8 | 26.9 | 0.1 | 27.3 | 0.4 | 27.6 | 0.3 | 28.0 | 0.4 |
| | 5 | 25.5 | 26.2 | 0.7 | 27.0 | 0.8 | 27.0 | 0.0 | 27.4 | 0.4 |
| | 6 | 28.2 | 28.5 | 0.3 | 29.1 | 0.6 | 29.1 | 0.0 | 29.7 | 0.6 |
| | 7 | 28.1 | 28.6 | 0.5 | 29.1 | 0.5 | 29.2 | 0.1 | 29.9 | 0.7 |
| | 8 | 27.0 | 28.1 | 1.1 | 28.7 | 0.6 | 28.9 | 0.2 | 29.3 | 0.4 |
| | 9 | 30.4 | 30.6 | 0.2 | 31.0 | 0.4 | 31.2 | 0.2 | 32.1 | 0.9 |
| | 10 | 28.4 | 29.0 | 0.6 | 29.8 | 0.8 | 29.8 | 0.0 | 30.3 | 0.5 |
| | Average | 28.30 | 28.87 | 0.57 | 29.44 | 0.57 | 29.62 | 0.18 | 30.28 | 0.66 |
| | Total increase in 24 hours: | | | 1.98 | | | | | | |
| Capon 139 | 1 | 27.7 | 28.5 | 0.8 | 28.7 | 0.2 | 28.7 | 0.0 | 29.4 | 0.7 |
| | 2 | 27.0 | 27.4 | 0.4 | 28.5 | 1.1 | 28.5 | 0.0 | 28.6 | 0.1 |
| | 3 | 29.1 | 29.3 | 0.2 | 30.0 | 0.7 | 30.0 | 0.0 | 30.9 | 0.9 |
| | 4 | 28.2 | 29.0 | 0.8 | 29.2 | 0.2 | 29.4 | 0.2 | 29.9 | 0.5 |
| | 5 | 27.6 | 27.8 | 0.2 | 29.2 | 1.4 | 29.3 | 0.1 | 29.9 | 0.6 |
| | 6 | 27.2 | 27.9 | 0.7 | 28.8 | 0.9 | 28.8 | 0.0 | 29.9 | 1.1 |
| | 7 | 24.7 | 25.8 | 1.1 | 26.3 | 0.5 | 26.5 | 0.2 | 27.4 | 0.9 |
| | 8 | 27.5 | 28.5 | 1.0 | 29.0 | 0.5 | 29.0 | 0.0 | 29.6 | 0.6 |
| | 9 | 28.0 | 28.6 | 0.6 | 29.4 | 0.8 | 29.4 | 0.0 | 30.2 | 0.8 |
| | 10 | 26.7 | 27.1 | 0.4 | 27.8 | 0.7 | 27.8 | 0.0 | 29.1 | 1.3 |
| | Average | 27.37 | 27.99 | 0.62 | 28.69 | 0.70 | 28.74 | 0.05 | 29.49 | 0.75 |
| | Total increase in 24 hours: | | | 2.12 | | | | | | |
| GRAND AVERAGE | | 27.36 | 27.92 | 0.56 | 28.56 | 0.64 | 28.68 | 0.12 | 29.44 | 0.76 |

AVERAGE TOTAL INCREASE IN 24 HOURS: 2.08

TABLE 4

TWELVE O'CLOCK BASIS. SECOND SERIES OF MEASUREMENTS OF THE SAME FEATHERS AS IN TABLE 3. TWENTY-EIGHTH DAY OF REGENERATION

| | | 1 12 NOON | 2 6 P. M. | INC. | 3 12 P. M. | INC. | 4 6 A. M. | INC. | 5 12 NOON | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon | 1 | 33.7 | 34.1 | 0.4 | 35.1 | 1.0 | 35.4 | 0.3 | 36.8 | 1.4 |
| 148 | 2 | 32.8 | 33.0 | 0.2 | 33.5 | 0.5 | 33.8 | 0.3 | 34.7 | 0.9 |
| | 3 | 33.0 | 33.5 | 0.5 | 34.1 | 0.6 | 34.3 | 0.2 | 34.7 | 0.4 |
| | 4 | 34.5 | 35.0 | 0.5 | 35.3 | 0.3 | 35.3 | 0.0 | 36.5 | 1.2 |
| | 5 | 30.6 | 31.5 | 0.9 | 31.9 | 0.4 | 32.5 | 0.6 | 33.4 | 0.9 |
| | 6 | 32.5 | 32.7 | 0.2 | 33.3 | 0.6 | 33.3 | 0.0 | 34.4 | 1.1 |
| | 7 | 32.2 | 32.6 | 0.4 | 33.3 | 0.7 | 33.4 | 0.1 | 33.8 | 0.4 |
| | 8 | 32.8 | 33.4 | 0.6 | 33.8 | 0.4 | 34.4 | 0.6 | 34.7 | 0.3 |
| | 9 | 32.0 | 32.3 | 0.3 | 32.8 | 0.5 | 32.8 | 0.0 | 33.7 | 0.9 |
| | 10 | 36.6 | 37.4 | 0.8 | 37.7 | 0.3 | 37.8 | 0.1 | 38.7 | 0.9 |
| | Average | 33.07 | 33.55 | 0.48 | 34.08 | 0.53 | 34.30 | 0.22 | 35.14 | 0.84 |
| | Total increase in 24 hours: | | | 2.07 | | | | | | |
| Capon | 1 | 33.3 | 34.4 | 1.1 | 35.6 | 1.2 | 35.6 | 0.0 | 35.8 | 0.2 |
| 171 | 2 | 39.0 | 39.2 | 0.2 | 39.6 | 0.4 | 39.9 | 0.3 | 41.1 | 1.2 |
| | 3 | 34.0 | 34.5 | 0.5 | 35.3 | 0.8 | 35.3 | 0.0 | 36.0 | 0.7 |
| | 4 | 31.3 | 32.2 | 0.9 | 32.6 | 0.4 | 32.6 | 0.0 | 33.4 | 0.8 |
| | 5 | 31.4 | 32.2 | 0.8 | 32.6 | 0.4 | 32.8 | 0.2 | 33.4 | 0.6 |
| | 6 | 33.5 | 35.2 | 1.7 | 35.5 | 0.3 | 35.5 | 0.0 | 36.0 | 0.5 |
| | 7 | 34.1 | 34.9 | 0.8 | 35.5 | 0.6 | 35.5 | 0.0 | 35.9 | 0.4 |
| | 8 | 33.5 | 34.8 | 1.3 | 34.9 | 0.1 | 35.2 | 0.3 | 35.9 | 0.7 |
| | 9 | 35.5 | 36.4 | 0.9 | 36.8 | 0.4 | 36.8 | 0.0 | 37.9 | 1.1 |
| | 10 | 34.0 | 34.7 | 0.7 | 35.3 | 0.6 | 35.3 | 0.0 | 36.0 | 0.7 |
| | Average | 33.96 | 34.85 | 0.89 | 35.37 | 0.52 | 35.45 | 0.08 | 36.14 | 0.69 |
| | Total increase in 24 hours: | | | 2.18 | | | | | | |
| Capon | 1 | 33.5 | 34.7 | 1.2 | 34.9 | 0.2 | 35.2 | 0.3 | 35.5 | 0.3 |
| 139 | 2 | 31.2 | 32.0 | 0.8 | 33.0 | 1.0 | 33.0 | 0.0 | 33.4 | 0.4 |
| | 3 | 35.1 | 35.5 | 0.4 | 36.5 | 1.0 | 36.9 | 0.4 | 37.5 | 0.6 |
| | 4 | 32.1 | 32.3 | 0.2 | 32.8 | 0.5 | 32.9 | 0.1 | 33.2 | 0.3 |
| | 5 | 33.2 | 33.9 | 0.7 | 35.0 | 1.1 | 35.0 | 0.0 | 35.4 | 0.4 |
| | 6 | 33.1 | 33.9 | 0.8 | 35.0 | 1.1 | 35.1 | 0.1 | 35.7 | 0.6 |
| | 7 | 30.8 | 31.4 | 0.6 | 31.7 | 0.3 | 32.0 | 0.3 | 32.9 | 0.9 |
| | 8 | 33.7 | 34.6 | 0.9 | 34.7 | 0.1 | 34.7 | 0.0 | 35.2 | 0.5 |
| | 9 | 34.2 | 34.8 | 0.6 | 35.3 | 0.5 | 35.3 | 0.0 | 35.8 | 0.5 |
| | 10 | 32.7 | 33.4 | 0.7 | 33.9 | 0.5 | 33.9 | 0.0 | 34.8 | 0.9 |
| | Average | 32.96 | 33.65 | 0.69 | 34.28 | 0.63 | 34.40 | 0.12 | 34.94 | 0.54 |
| | Total increase in 24 hours: | | | 1.98 | | | | | | |
| GRAND AVERAGE | | 33.33 | 34.02 | 0.69 | 34.58 | 0.56 | 34.72 | 0.14 | 35.41 | 0.69 |

AVERAGE TOTAL INCREASE IN 24 HOURS: 2.08

Measurements were made to the nearest tenth of a millimeter as follows: A piece of white paper was inserted beneath the feather which was then held flat against it, and an original measurement was made with spring nut outside calipers from the mouth of the follicle on the upper side to the tip of the feather. The space between the points of the spring calipers was then measured with vernier calipers with direct gauge reading to 0.1 mm. (made by Schietrumpf of Jena). The part of the feather within the follicle (about 7 mm. in length) was not taken into account. The principal sources of error by this method are, first, that the position of the points of the spring calipers in the original measurements must be judged by the eye alone, and, second, the assumption is made that the opening of the follicle maintains a fixed position during the 24 hours. These possible sources of error tend to be averaged out. The very large averaged difference between the six-hour period from midnight to 6:00 A. M. and the other six-hour measurements are consistent for the separate measurements with some exceptions (see tables).

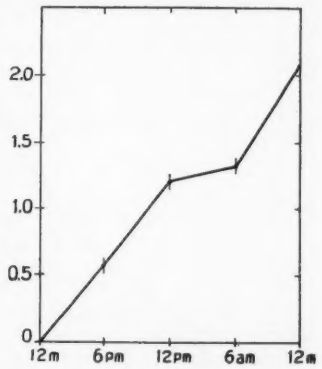


FIGURE 2

Saddle feathers. From data of table 3. The grand average of six-hour increments of the three birds plotted. Based on 12:00 o'clock. Ordinates = millimeters of growth; abscissae = time of day.

The average growth in 24 hours of all breast feathers in both sets of determinations was 2.58 mm.; for all saddle feathers, 2.08 mm. If the growth in each six-hour period in the diurnal cycle were uniform, each would record 25% of this amount. The actual percentages,[1] averaging all determinations for each six-hour period for breast and for saddle, were as follows:

| | BREAST | SADDLE |
|---|---|---|
| 12:00 noon to 6:00 P. M. | 31% | 30% |
| 6:00 P. M. to 12:00 midnight | 26% | 29% |
| 12:00 midnight to 6:00 A. M. | 9% | 6% |
| 6:00 A. M. to 12:00 noon | 34% | 35% |

It will be noted that the amount of depression of growth rate from midnight to 6:00 A. M. is greater in the saddle than in the breast. This is perhaps due to a lower threshold of susceptibility similar to that which Juhn and Gustavson ('30) found in saddle as compared with breast feathers

[1] The nearest whole number is used for each percentage.

in the case of reaction to the female hormone, and which they attributed to slower rate of growth.

It is interesting to note that 50 zero increments are recorded between midnight and 6:00 A. M. out of the 120 records made for this period, only one between noon and 6:00 P. M., two between 6:00 P. M. and midnight and none between 6:00 A. M. and noon, similarly out of 120 records for each period. Two of the determinations for six-hour periods are small decrements, 0.1 and 0.2, respectively, obviously due to errors of recording. There are five records between midnight and 6:00 A. M. out of 120 in which the increment of individual feathers exceeds 25% of the total growth for 24 hours. The range of variation of increment within each period is considerable. There are also slight differences to be noted between the three birds used.

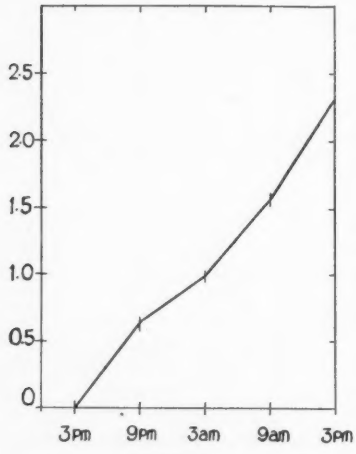


FIGURE 3

Breast feathers. From data of table 5. The grand average of six-hour increments of the three birds plotted. Based on 9:00 o'clock. Ordinates = millimeters of growth; abscissae = time of day.

Except for the disturbance due to measurement, the birds were on a normal régime with no artificial lighting. No attempt has been made to determine how differences in feeding, lighting or activity would affect the diurnal cycle.

2. *Six-Hour Increments Based on Nine O'Clock.*—The amount of growth was then measured at six-hour periods beginning at nine o'clock instead of twelve o'clock. The regeneration age at the beginning of the measurements was 20 days in the case of the breast feathers and 22 days in the case of the saddle feathers. The same three capons were used as before, and precisely the same methods were followed. The observations were made June 12–14 for the breast feathers (tables 5 and 6 and Fig. 3), and June 24–26 for the saddle feathers (tables 7 and 8 and Fig. 4). In each case two consecutive 24-hour periods were used. In the case of the measurements beginning at twelve o'clock, the two 24-hour periods were separated by three days in both breast and saddle feathers. The measurements for six-hour periods beginning at twelve o'clock were made in March and April when the temperature of the animal house was much lower than in the case of the periods based on nine o'clock, which were made in June. These differences may have had some effect.

TABLE 5

NINE O'CLOCK BASIS. JUNE 12–13, 1939. BREAST FEATHERS BROWN LEGHORN CAPONS. TWENTIETH DAY OF REGENERATION

| | | 1 9 A. M. | 2 3 P. M. | INC. | 3 9 P. M. | INC. | 4 3 A. M. | INC. | 5 9 A. M. | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon 148 | 1 | 20.3 | 21.1 | 0.8 | 21.7 | 0.6 | 22.0 | 0.3 | 22.1 | 0.1 |
| | 2 | 20.0 | 20.7 | 0.7 | 20.9 | 0.2 | 21.5 | 0.6 | 22.0 | 0.5 |
| | 3 | 20.1 | 21.5 | 1.4 | 22.2 | 0.7 | 22.2 | 0.0 | 22.4 | 0.2 |
| | 4 | 19.7 | 20.5 | 0.8 | 21.4 | 0.9 | 21.4 | 0.0 | 22.2 | 0.8 |
| | 5 | 18.9 | 19.8 | 0.9 | 21.2 | 1.4 | 21.3 | 0.1 | 22.0 | 0.7 |
| | 6 | 18.0 | 18.8 | 0.8 | 19.5 | 0.7 | 20.2 | 0.7 | 20.7 | 0.5 |
| | 7 | 18.0 | 18.8 | 0.8 | 19.5 | 0.7 | 20.5 | 1.0 | 21.3 | 0.8 |
| | 8 | 18.9 | 19.7 | 0.8 | 20.4 | 0.7 | 20.8 | 0.4 | 21.3 | 0.5 |
| | 9 | 18.7 | 19.8 | 1.1 | 20.4 | 0.6 | 20.8 | 0.4 | 21.3 | 0.5 |
| | 10 | 16.7 | 17.7 | 1.0 | 17.9 | 0.2 | 18.3 | 0.4 | 19.1 | 0.8 |
| Average | | 18.93 | 19.84 | 0.91 | 20.51 | 0.67 | 20.90 | 0.39 | 21.44 | 0.54 |
| Total increase in 24 hours: | | | 2.51 | | | | | | | |
| Capon 171 | 1 | 16.6 | 17.4 | 0.8 | 18.0 | 0.6 | 18.0 | 0.0 | 18.7 | 0.7 |
| | 2 | 16.6 | 17.4 | 0.8 | 18.0 | 0.6 | 18.4 | 0.4 | 19.4 | 1.0 |
| | 3 | 16.0 | 16.5 | 0.5 | 17.0 | 0.5 | 17.5 | 0.5 | 18.0 | 0.5 |
| | 4 | 15.0 | 15.9 | 0.9 | 16.3 | 0.4 | 16.9 | 0.6 | 17.6 | 0.7 |
| | 5 | 15.5 | 16.1 | 0.6 | 17.2 | 1.1 | 17.6 | 0.4 | 17.9 | 0.3 |
| | 6 | 15.2 | 15.8 | 0.6 | 16.7 | 0.9 | 17.6 | 0.9 | 17.7 | 0.1 |
| | 7 | 15.0 | 15.6 | 0.6 | 15.9 | 0.3 | 16.5 | 0.6 | 16.7 | 0.2 |
| | 8 | 15.8 | 16.8 | 1.0 | 17.4 | 0.6 | 17.4 | 0.0 | 18.3 | 0.9 |
| | 9 | 15.6 | 16.7 | 1.1 | 17.6 | 0.9 | 17.9 | 0.3 | 18.4 | 0.5 |
| | 10 | 13.7 | 14.6 | 0.9 | 15.3 | 0.7 | 15.3 | 0.0 | 16.4 | 1.1 |
| Average | | 15.50 | 16.28 | 0.78 | 16.94 | 0.66 | 17.31 | 0.37 | 17.91 | 0.60 |
| Total increase in 24 hours: | | | 2.41 | | | | | | | |
| Capon 139 | 1 | 20.2 | 20.6 | 0.4 | 20.8 | 0.2 | 20.9 | 0.1 | 21.5 | 0.6 |
| | 2 | 20.3 | 21.1 | 0.8 | 21.5 | 0.4 | 21.6 | 0.1 | 21.9 | 0.3 |
| | 3 | 17.5 | 18.1 | 0.6 | 18.6 | 0.5 | 18.9 | 0.3 | 19.3 | 0.4 |
| | 4 | 21.1 | 21.7 | 0.6 | 22.2 | 0.5 | 22.3 | 0.1 | 23.1 | 0.8 |
| | 5 | 19.7 | 20.6 | 0.9 | 21.5 | 0.9 | 21.5 | 0.0 | 21.9 | 0.4 |
| | 6 | 21.0 | 21.5 | 0.5 | 22.1 | 0.6 | 22.9 | 0.8 | 23.3 | 0.4 |
| | 7 | 19.7 | 20.4 | 0.7 | 20.9 | 0.5 | 21.4 | 0.5 | 21.8 | 0.4 |
| | 8 | 20.7 | 21.2 | 0.5 | 21.9 | 0.7 | 22.9 | 1.0 | 23.3 | 0.4 |
| | 9 | 19.7 | 20.0 | 0.3 | 20.8 | 0.8 | 20.9 | 0.1 | 21.7 | 0.8 |
| | 10 | 18.9 | 19.4 | 0.5 | 19.8 | 0.4 | 20.1 | 0.3 | 21.2 | 1.1 |
| Average | | 19.88 | 20.46 | 0.58 | 21.01 | 0.55 | 21.34 | 0.33 | 21.90 | 0.56 |
| Total increase in 24 hours: | | | 2.02 | | | | | | | |
| GRAND AVERAGE | | 18.10 | 18.86 | 0.76 | 19.49 | 0.63 | 19.85 | 0.36 | 20.42 | 0.57 |
| AVERAGE TOTAL INCREASE IN 24 HOURS: 2.32 | | | | | | | | | | |

TABLE 6

NINE O'CLOCK BASIS. SECOND SERIES OF MEASUREMENTS OF THE SAME FEATHERS AS IN TABLE 5. TWENTY-FIRST DAY OF REGENERATION

| | | 1 9 A. M. | 2 3 P. M. | INC. | 3 9 P. M. | INC. | 4 3 A. M. | INC. | 5 9 A. M. | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon | 1 | 22.1 | 22.8 | 0.7 | 23.3 | 0.5 | 23.5 | 0.2 | 24.7 | 1.2 |
| 148 | 2 | 22.0 | 22.4 | 0.4 | 22.8 | 0.4 | 23.5 | 0.7 | 24.5 | 1.0 |
| | 3 | 22.4 | 23.4 | 1.0 | 23.9 | 0.5 | 24.2 | 0.3 | 25.1 | 0.9 |
| | 4 | 22.2 | 22.5 | 0.3 | 23.3 | 0.8 | 23.4 | 0.1 | 24.2 | 0.8 |
| | 5 | 22.0 | 22.4 | 0.4 | 23.2 | 0.8 | 23.5 | 0.3 | 24.2 | 0.7 |
| | 6 | 20.7 | 21.4 | 0.7 | 21.9 | 0.5 | 22.6 | 0.7 | 23.3 | 0.7 |
| | 7 | 21.3 | 21.7 | 0.4 | 22.7 | 1.0 | 23.2 | 0.5 | 23.7 | 0.5 |
| | 8 | 21.3 | 22.2 | 0.9 | 22.7 | 0.5 | 23.2 | 0.5 | 24.0 | 0.8 |
| | 9 | 21.3 | 22.2 | 0.9 | 22.7 | 0.5 | 23.0 | 0.3 | 24.1 | 1.1 |
| | 10 | 19.1 | 20.0 | 0.9 | 20.2 | 0.2 | 21.0 | 0.8 | 21.6 | 0.6 |
| | Average | 21.44 | 22.10 | 0.66 | 22.67 | 0.57 | 23.11 | 0.44 | 23.94 | 0.83 |
| | Total increase in 24 hours: | | | 2.50 | | | | | | |
| Capon | 1 | 18.7 | 19.8 | 1.1 | 20.1 | 0.3 | 20.8 | 0.7 | 21.5 | 0.7 |
| 171 | 2 | 19.4 | 20.5 | 1.1 | 20.8 | 0.3 | 21.5 | 0.7 | 21.6 | 0.1 |
| | 3 | 18.0 | 18.6 | 0.6 | 19.2 | 0.6 | 20.0 | 0.8 | 20.5 | 0.5 |
| | 4 | 17.6 | 18.5 | 0.9 | 18.8 | 0.3 | 19.4 | 0.6 | 20.0 | 0.6 |
| | 5 | 17.9 | 19.0 | 1.1 | 19.6 | 0.6 | 20.4 | 0.8 | 20.8 | 0.4 |
| | 6 | 17.7 | 18.5 | 0.8 | 19.3 | 0.8 | 19.6 | 0.3 | 20.0 | 0.4 |
| | 7 | 16.7 | 17.6 | 0.9 | 18.5 | 0.9 | 18.8 | 0.3 | 19.5 | 0.7 |
| | 8 | 18.3 | 19.0 | 0.7 | 19.8 | 0.8 | 20.2 | 0.4 | 20.9 | 0.7 |
| | 9 | 18.4 | 19.5 | 1.1 | 20.2 | 0.7 | 20.7 | 0.5 | 21.5 | 0.8 |
| | 10 | 16 4 | 17.2 | 0.8 | 17.5 | 0.3 | 18.0 | 0.5 | 18.6 | 0.6 |
| | Average | 17.91 | 18.82 | 0.91 | 19.38 | 0.56 | 19.94 | 0.56 | 20.49 | 0.55 |
| | Total increase in 24 hours: | | | 2.58 | | | | | | |
| Capon | 1 | 21.5 | 22.5 | 1.0 | 23.1 | 0.6 | 23.7 | 0.6 | 24.3 | 0.6 |
| 139 | 2 | 21.9 | 22.8 | 0.9 | 23.5 | 0.7 | 23.7 | 0.2 | 24.3 | 0.6 |
| | 3* | 18.9 | 19.6 | 0.7 | 20.0 | 0.4 | 20.4 | 0.4 | 21.6 | 1.2 |
| | 4 | 23.1 | 23.7 | 0.6 | 24.4 | 0.7 | 24.8 | 0.4 | 25.4 | 0.6 |
| | 5 | 21.9 | 22.3 | 0.4 | 22.9 | 0.6 | 23.4 | 0.5 | 23.8 | 0.4 |
| | 6 | 23.3 | 24.1 | 0.8 | 24.7 | 0.6 | 25.4 | 0.7 | 25.6 | 0.2 |
| | 7 | 21.8 | 22.4 | 0.6 | 23.2 | 0.8 | 23.5 | 0.3 | 24.3 | 0.8 |
| | 8 | 23.3 | 23.5 | 0.2 | 24.3 | 0.8 | 24.6 | 0.3 | 25.7 | 1.1 |
| | 9 | 21.7 | 22.5 | 0.8 | 22.8 | 0.3 | 23.4 | 0.6 | 24.5 | 1.1 |
| | 10 | 21.2 | 21.5 | 0.3 | 22.0 | 0.5 | 22.4 | 0.4 | 23.5 | 1.1 |
| | Average | 21.86 | 22.49 | 0.63 | 23.09 | 0.60 | 23.53 | 0.44 | 24.30 | 0.77 |
| | Total increase in 24 hours: | | | 2.44 | | | | | | |
| GRAND AVERAGE | | 20.40 | 21.13 | 0.73 | 21.71 | 0.58 | 22.19 | 0.48 | 22.91 | 0.72 |

AVERAGE TOTAL INCREASE IN 24 HOURS: 2.51

* A newly selected feather to replace the one used in the first series of measurements (table 5) which was lost.

TABLE 7

NINE O'CLOCK BASIS. JUNE 24–25, 1939. SADDLE FEATHERS BROWN LEGHORN CAPONS. TWENTY-SECOND DAY OF REGENERATION

| | | 1 9 A. M. | 2 3 P. M. | INC. | 3 9 P. M. | INC. | 4 3 A. M. | INC. | 5 9 A. M. | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon 148 | 1 | 27.7 | 28.2 | 0.5 | 28.7 | 0.5 | 28.8 | 0.1 | 29.3 | 0.5 |
| | 2 | 17.4 | 17.9 | 0.5 | 18.2 | 0.3 | 18.7 | 0.5 | 19.1 | 0.4 |
| | 3 | 17.8 | 18.2 | 0.4 | 18.7 | 0.5 | 18.8 | 0.1 | 19.2 | 0.4 |
| | 4 | 18.9 | 19.5 | 0.6 | 19.7 | 0.2 | 19.9 | 0.2 | 20.6 | 0.7 |
| | 5 | 12.3 | 13.2 | 0.9 | 13.6 | 0.4 | 14.0 | 0.4 | 14.7 | 0.7 |
| | 6 | 14.3 | 15.2 | 0.9 | 15.9 | 0.7 | 15.9 | 0.0 | 16.3 | 0.4 |
| | 7 | 14.1 | 14.8 | 0.7 | 15.1 | 0.3 | 15.2 | 0.1 | 15.8 | 0.6 |
| | 8 | 14.1 | 14.8 | 0.7 | 15.1 | 0.3 | 15.5 | 0.4 | 16.2 | 0.7 |
| | 9 | 14.9 | 15.2 | 0.3 | 15.8 | 0.6 | 16.2 | 0.4 | 16.7 | 0.5 |
| | 10 | 16.1 | 16.4 | 0.3 | 16.7 | 0.3 | 16.9 | 0.2 | 17.3 | 0.4 |
| Average | | 16.76 | 17.34 | 0.58 | 17.75 | 0.41 | 17.99 | 0.24 | 18.52 | 0.53 |
| Total increase in 24 hours: | | | 1.76 | | | | | | | |
| Capon 171 | 1 | 17.8 | 18.4 | 0.6 | 18.9 | 0.5 | 19.1 | 0.2 | 19.6 | 0.5 |
| | 2 | 18.4 | 19.0 | 0.6 | 19.5 | 0.5 | 19.6 | 0.1 | 20.2 | 0.6 |
| | 3 | 17.5 | 17.8 | 0.3 | 18.5 | 0.7 | 18.7 | 0.2 | 19.3 | 0.6 |
| | 4 | 16.5 | 16.9 | 0.4 | 17.4 | 0.5 | 17.6 | 0.2 | 18.2 | 0.6 |
| | 5 | 18.4 | 18.7 | 0.3 | 19.3 | 0.6 | 19.5 | 0.2 | 20.1 | 0.6 |
| | 6 | 18.7 | 19.0 | 0.3 | 19.5 | 0.5 | 19.6 | 0.1 | 20.5 | 0.9 |
| | 7 | 15.5 | 16.2 | 0.7 | 16.8 | 0.6 | 17.2 | 0.4 | 17.5 | 0.3 |
| | 8 | 18.6 | 19.4 | 0.8 | 19.8 | 0.4 | 20.1 | 0.3 | 20.4 | 0.3 |
| | 9 | 17.5 | 18.4 | 0.9 | 18.6 | 0.2 | 18.7 | 0.1 | 19.7 | 1.0 |
| | 10 | 16.8 | 17.5 | 0.7 | 18.0 | 0.5 | 18.4 | 0.4 | 18.8 | 0.4 |
| Average | | 17.57 | 18.13 | 0.56 | 18.63 | 0.50 | 18.85 | 0.22 | 19.43 | 0.58 |
| Total increase in 24 hours: | | | 1.86 | | | | | | | |
| Capon 139 | 1 | 15.7 | 16.0 | 0.3 | 17.0 | 1.0 | 17.3 | 0.3 | 17.9 | 0.6 |
| | 2 | 14.7 | 15.3 | 0.6 | 15.9 | 0.6 | 16.0 | 0.1 | 16.6 | 0.6 |
| | 3 | 24.5 | 25.1 | 0.6 | 25.4 | 0.3 | 25.8 | 0.4 | 26.3 | 0.5 |
| | 4 | 15.5 | 16.0 | 0.5 | 16.7 | 0.7 | 17.0 | 0.3 | 17.6 | 0.6 |
| | 5 | 15.5 | 16.1 | 0.6 | 16.5 | 0.4 | 16.8 | 0.3 | 17.3 | 0.5 |
| | 6 | 17.1 | 17.5 | 0.4 | 18.3 | 0.8 | 18.4 | 0.1 | 19.1 | 0.7 |
| | 7 | 17.8 | 18.5 | 0.7 | 18.8 | 0.3 | 19.3 | 0.5 | 19.9 | 0.6 |
| | 8 | 14.6 | 15.5 | 0.9 | 16.0 | 0.5 | 16.3 | 0.3 | 16.7 | 0.4 |
| | 9 | 14.8 | 15.8 | 1.0 | 16.1 | 0.3 | 16.3 | 0.2 | 16.7 | 0.4 |
| | 10 | 17.2 | 17.8 | 0.6 | 18.1 | 0.3 | 18.5 | 0.4 | 19.1 | 0.6 |
| Average | | 16.74 | 17.36 | 0.62 | 17.88 | 0.52 | 18.17 | 0.29 | 18.72 | 0.55 |
| Total increase in 24 hours: | | | 1.98 | | | | | | | |
| GRAND AVERAGE | | 17.02 | 17.61 | 0.59 | 18.09 | 0.48 | 18.34 | 0.25 | 18.89 | 0.55 |

AVERAGE TOTAL INCREASE IN 24 HOURS: 1.87

TABLE 8

NINE O'CLOCK BASIS. SECOND SERIES OF MEASUREMENTS OF THE SAME FEATHERS AS IN TABLE 7. TWENTY-THIRD DAY OF REGENERATION

| | | 1 9 A. M. | 2 3 P. M. | INC. | 3 9 P. M. | INC. | 4 3 A. M. | INC. | 5 9 A. M. | INC. |
|---|---|---|---|---|---|---|---|---|---|---|
| Capon 148 | 1 | 29.3 | 30.2 | 0.9 | 30.6 | 0.4 | 31.0 | 0.4 | 31.7 | 0.7 |
| | 2 | 19.1 | 19.8 | 0.7 | 20.3 | 0.5 | 20.3 | 0.0 | 21.0 | 0.7 |
| | 3 | 19.2 | 19.8 | 0.6 | 20.6 | 0.8 | 21.0 | 0.4 | 21.7 | 0.7 |
| | 4 | 20.6 | 21.2 | 0.6 | 22.4 | 1.2 | 22.4 | 0.0 | 23.4 | 1.0 |
| | 5 | 14.7 | 15.1 | 0.4 | 15.6 | 0.5 | 16.2 | 0.6 | 16.6 | 0.4 |
| | 6 | 16.3 | 17.0 | 0.7 | 17.4 | 0.4 | 17.9 | 0.5 | 18.8 | 0.9 |
| | 7 | 15.8 | 16.1 | 0.3 | 17.0 | 0.9 | 17.7 | 0.7 | 18.1 | 0.4 |
| | 8 | 16.2 | 16.7 | 0.5 | 16.9 | 0.2 | 16.9 | 0.0 | 17.7 | 0.8 |
| | 9 | 16.7 | 17.4 | 0.7 | 18.2 | 0.8 | 18.5 | 0.3 | 18.9 | 0.4 |
| | 10 | 17.3 | 17.9 | 0.6 | 18.6 | 0.7 | 19.0 | 0.4 | 19.5 | 0.5 |
| | Average | 18.52 | 19.12 | 0.60 | 19.76 | 0.64 | 20.09 | 0.33 | 20.74 | 0.65 |
| | Total increase in 24 hours: | | | 2.22 | | | | | | |
| Capon 171 | 1 | 19.6 | 20.2 | 0.6 | 20.6 | 0.4 | 21.2 | 0.6 | 21.6 | 0.4 |
| | 2 | 20.2 | 20.6 | 0.4 | 21.2 | 0.6 | 21.3 | 0.1 | 21.9 | 0.6 |
| | 3 | 19.3 | 19.7 | 0.4 | 20.0 | 0.3 | 20.3 | 0.3 | 20.8 | 0.5 |
| | 4 | 18.2 | 18.6 | 0.4 | 19.4 | 0.8 | 19.5 | 0.1 | 20.0 | 0.5 |
| | 5 | 20.1 | 20.8 | 0.7 | 21.5 | 0.7 | 21.8 | 0.3 | 22.4 | 0.6 |
| | 6 | 20.5 | 21.3 | 0.8 | 21.8 | 0.5 | 21.8 | 0.0 | 22.5 | 0.7 |
| | 7 | 17.5 | 18.0 | 0.5 | 18.7 | 0.7 | 19.0 | 0.3 | 19.7 | 0.7 |
| | 8 | 20.4 | 21.6 | 1.2 | 22.1 | 0.5 | 22.5 | 0.4 | 23.0 | 0.5 |
| | 9 | 19.7 | 20.2 | 0.5 | 20.8 | 0.6 | 21.0 | 0.2 | 21.5 | 0.5 |
| | 10 | 18.8 | 19.4 | 0.6 | 19.8 | 0.4 | 20.3 | 0.5 | 20.9 | 0.6 |
| | Average | 19.43 | 20.04 | 0.61 | 20.59 | 0.55 | 20.87 | 0.28 | 21.43 | 0.56 |
| | Total increase in 24 hours: | | | 2.00 | | | | | | |
| Capon 139 | 1 | 17.9 | 18.4 | 0.5 | 18.9 | 0.5 | 19.2 | 0.3 | 20.0 | 0.8 |
| | 2 | 16.6 | 17.1 | 0.5 | 17.5 | 0.4 | 17.7 | 0.2 | 18.5 | 0.8 |
| | 3 | 26.3 | 26.7 | 0.4 | 27.5 | 0.8 | 27.9 | 0.4 | 28.1 | 0.2 |
| | 4 | 17.6 | 18.4 | 0.8 | 18.7 | 0.3 | 19.1 | 0.4 | 19.8 | 0.7 |
| | 5 | 17.3 | 17.7 | 0.4 | 18.0 | 0.3 | 18.4 | 0.4 | 19.1 | 0.7 |
| | 6 | 19.1 | 19.9 | 0.8 | 20.4 | 0.5 | 20.5 | 0.1 | 21.1 | 0.6 |
| | 7 | 19.9 | 20.2 | 0.3 | 20.8 | 0.6 | 20.8 | 0.0 | 21.7 | 0.9 |
| | 8 | 16.7 | 17.4 | 0.7 | 18.0 | 0.6 | 18.1 | 0.1 | 18.9 | 0.8 |
| | 9 | 16.7 | 17.4 | 0.7 | 18.0 | 0.6 | 18.4 | 0.4 | 19.0 | 0.6 |
| | 10 | 19.1 | 19.9 | 0.8 | 20.6 | 0.7 | 21.0 | 0.4 | 21.4 | 0.4 |
| | Average | 18.72 | 19.31 | 0.59 | 19.84 | 0.53 | 20.11 | 0.27 | 20.76 | 0.65 |
| | Total increase in 24 hours: | | | 2.04 | | | | | | |
| GRAND AVERAGE | | 18.89 | 19.49 | 0.60 | 20.06 | 0.57 | 20.36 | 0.30 | 20.98 | 0.62 |

AVERAGE TOTAL INCREASE IN 24 HOURS: 2.09

The average growth in 24 hours of all breast feathers in both sets of determinations was 2.15 mm., of all saddle feathers, 1.98 mm., in each case somewhat less than the previous sets. The averages of percentages of daily increments for six-hour periods were as follows:

| | BREAST | | SADDLE | |
|---|---|---|---|---|
| | 1ST DAY | 2ND DAY | 1ST DAY | 2ND DAY |
| 9:00 A. M. to 3:00 P. M. | 32.76 | 29.08 | 31.55 | 28.70 |
| 3:00 P. M. to 9:00 P. M. | 27.15 | 23.11 | 25.67 | 27.27 |
| 9:00 P. M. to 3:00 A. M. | 15.52 | 19.12 | 13.37 | 14.36 |
| 3:00 A. M. to 9:00 A. M. | 24.57 | 28.69 | 29.41 | 29.67 |

There is a depression of growth rate here from 9:00 P. M. to 3:00 A. M. but of a lesser order of magnitude than from 12:00 midnight to 6:00 A. M. in the former series (cf. Figs. 1 to 4).

3. *Comparison of the Twelve O'Clock and Nine O'Clock Bases.*— Growth within each six-hour period is necessarily represented as uniform owing to the requirements of the method; but it is obviously improbable in the highest degree that this is actually the case. The purpose of repeating the original observations made on a twelve o'clock basis by another set of observations based on nine o'clock was to ascertain whether by comparison it would be possible to determine at least the three-hour period with the lowest rate of growth. The remainder of the diurnal curves of growth (cf. Figs. 1 to 4) does not exhibit sufficient variation to encourage an attempt at closer determination of the time of maximum rate of growth.

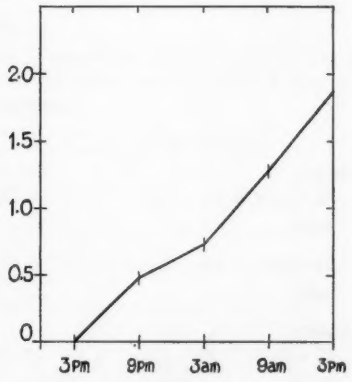


FIGURE 4

Saddle feathers. From data of table 7. The grand average of six-hour increments of the three birds plotted. Based on 9:00 o'clock. Ordinates = millimeters of growth; abscissae = time of day.

In table 9 we have divided the growth of each six-hour period into equal halves, thus establishing arbitrary three-hour periods of growth both on the twelve o'clock and the nine o'clock bases; these figures are taken from the grand averages of the first set of measurements in each case, and the corresponding three-hour periods for the two bases are thus brought directly into comparison. It will be seen that except for the periods of depression of growth rates, 12:00 P. M. to 6:00 A. M. on the twelve o'clock basis, and 9:00 P. M. to 3:00 A. M. on the nine o'clock basis, the three-hour periods

agree fairly well in the two series. In spite of the great discrepancies between the twelve o'clock and the nine o'clock bases during the periods of depression, it is nevertheless shown by the table that the sum of the amount of growth on the two bases in the three-hour period from 12:00 P. M. to 3:00 A. M. is much less than in any other three-hour period, even comparing the two adjacent three-hour periods. We would therefore conclude that the period of least growth is from midnight to 3:00 A. M.

This reinforces the conclusion that the diurnal curve of growth is in reality a flowing, and not an angular, curve. We have attempted to apply this conception by the triangular signs in table 9. These are intended to indicate that on the twelve o'clock basis the growth from 6:00 P. M. to 9:00 P. M. is probably more than from 9:00 P. M. to midnight, and that the

TABLE 9

DATA REARRANGED ON THE BASIS OF THREE-HOUR INCREMENTS. ALL DATA BASED ON THE AVERAGE OF THE FIRST SET OF MEASUREMENTS OF ALL THE THREE BROWN LEGHORN CAPONS USED

| | 12 M.–3 P. M. | 3 P. M.–6 P. M. | 6 P. M.–9 P. M. | 9 P. M.–12 P. M. | 12 P. M.–3 A. M. | 3 A. M.–6 A. M. | 6 A. M.–9 A. M. | 9 A. M.–12 M. | TOTAL INC. |
|---|---|---|---|---|---|---|---|---|---|
| **Breast** | | | | | | | | | |
| 12 o'clock basis | 0.40 | 0.40 | 0.33 | 0.33 | 0.12 | 0.12 | 0.47 | 0.47 | 2.64 mm. |
| 9 o'clock basis | 0.38 | 0.315 | 0.315 | 0.18 | 0.18 | 0.285 | 0.285 | 0.38 | 2.32 mm. |
| **Saddle** | | | | | | | | | |
| 12 o'clock basis | 0.28 | 0.28 | 0.32 | 0.32 | 0.06 | 0.06 | 0.38 | 0.38 | 2.08 mm. |
| 9 o'clock basis | 0.295 | 0.24 | 0.24 | 0.125 | 0.125 | 0.275 | 0.275 | 0.295 | 1.87 mm. |

growth from midnight to 3:00 A. M. is probably less than from 3:00 A. M. to 6:00 A. M. Similarly, on the nine o'clock basis the growth from 9:00 P. M. to midnight is probably more than from midnight to 3:00 A. M., and the growth from 3:00 A. M. to 6:00 A. M. less than from 6:00 A. M. to 9:00 A. M. Any corrections made in this sense would tend to even out the discrepancies between the two bases.

In figures 5 and 6 we have applied the principle of these corrections to the curves of growth for the breast feathers on the twelve o'clock and nine o'clock bases respectively (Figs. 1 and 2). The corrections are indicated by the flowing dotted curves crossing the original curves. The exact form of the dotted curve represents merely our best judgment of the amount and distribution of the corrections, and to that extent is arbitrary, but it is

believed to give a more correct representation of the actual growth rate than either of the unmodified curves. The six-hour period of least growth is emphasized by the stippled triangle below it. The 3:00 A. M. ordinate divides it into unequal parts.

## III. Discussion

1. *The Physiological Basis of the Diurnal Rhythm.*—(*a*) Diurnal fluctuations of basal metabolism. The determinations of Barott and others ('38)[1] of the diurnal fluctuations of the energy production and gaseous metabolism of male Rhode Island chickens aged from four to 130 days are by far the most thorough on record. On page 158 they give a curve of the diurnal rhythm of the energy metabolism, as measured by oxygen consumption, of fasting male Rhode Island Red chickens of between 15 and about 18 weeks of age. This is a very regular flowing curve covering three days. The high point of the curve occurs daily between 8:00 A. M. and 9:00 A. M. and the low point between 8:00 P. M. and 9:00 P. M. On the second day of the three-day record, the high oxygen consumption was about 0.85 cc. per hour per gram live weight, and the low about 0.72.

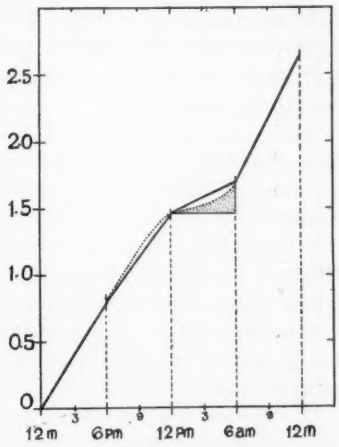


FIGURE 5

Breast feathers. The 12:00 o'clock basis (Fig. 1) modified by the dotted line based on comparison of the 9:00 o'clock basis (Fig. 3) as explained in table 9. The stippled area emphasizes the period of the least six-hour increment. Ordinates = millimeters of growth; abscissae = time of day.

Bacq ('29) studied four cocks both under normal feeding and fasting régimes. His curve of diurnal fluctuations of basal metabolism (calories per kg. hr.) is quite similar to those of Barott though the observations are rather fragmentary; the low and high points are slightly later.

If we attempt a closer comparison to the oxygen consumption curve of Barott *et al.* we find that the lowest three-hour period of oxygen consumption, which offers the best basis for comparison of growth in the 24-hour cycle, is, according to their determinations, between 6:00 P. M. and 9:00 P. M. approximately, whereas the period of least growth according to our determinations is between midnight and 3:00 A. M., thus six hours later.

[1] Cf. also Benedict, Landauer and Fox ('32), and Scharnke ('32).

If we assume that there is a causal relation between energy metabolism and growth in length of the feather, we have to find some explanation of the very considerable lag of effect.

Lillie and Juhn ('32) attempted to estimate the growth due to plasmatic growth, including cell-division, and to cell-differentiation, respectively, in the growth in length of the shaft (p. 143) and in the barbs (p. 150), and concluded that about 90% of growth in length is due to cell-differentiation and only about 10% to plasmatic growth. The amount of growth of the whole feather due to cell-differentiation, which consists, so far as magnitudes are concerned, in elongation and "ballooning" of cells, depends on the number of cells presented for differentiation as presumably the most important factor; and the number presented at any one time will depend on the rate of cell-division.

Even if the rate of cell-division should respond immediately to reduced $O_2$ in the blood, time would be required for the new cells to move up into the zone of differentiation, and before reduction in the number of cells available for differentiation becomes a measurable factor in reduction of rate of growth. It is therefore not to be expected that the dampening effects of lower metabolism will receive simultaneous response in measurements of length increments at six-hour intervals. A certain amount of lag is to be expected on the hypothesis of a causal relation between the rates of energy metabolism and growth increments in such a system as the regenerating feather.

(*b*) Diurnal fluctuations of body temperature. Regular diurnal fluctuations of internal body temperature have often been recorded. Simpson and Galbraith ('05) record a maximum temperature of 41.9°C. for Dorking males at 3:00 P. M. and a minimum temperature of 40.9° at 3:00 A. M. The temperature drops suddenly from 6:00 P. M. to 9:00 P. M. and then holds near, or below, 41° to about 4:00 A. M. Riddle ('07) similarly recorded a marked drop in temperature in fowl, ducks and pigeons during the night. Hilden and Stenback ('16) record a series of observations on fowl and eight other species of birds confirming in general the determinations of Simpson and Galbraith, but adding the valuable determination that the regular day and night variations are readily reversed by keeping the birds in the dark during the day and furnishing illumination at night. A more systematic study of the diurnal temperature fluctuations in fowl under various conditions is, however, still much to be desired.

As regards other birds, Simpson and Galbraith ('05) record a much greater depression of body temperature during the night than in fowl in a considerable number of species, especially smaller birds; but they found that in the case of the owl, a bird of nocturnal habit, the situation was reversed. Wetmore ('21) made an immense number of careful determinations of body temperatures of birds taken in the field, and found, as regards

diurnal variations, marked depressions during the night, with the exception of birds of nocturnal habit in which the situation was reversed, confirming Simpson and Galbraith.

Riley ('37) reports daily variation in the body temperature of the house sparrow ranging from an average of 110°F. during the day to 103–104°F. during the night. Spermatogenetic activity is limited to the period of reduced body temperature. Artificial inversion of light and dark periods with reference to normal day and night inverts also the normal day and night body temperatures and the time of spermatogenetic activity.

Huff ('39) has made a study of diurnal variation of temperature in canaries in connection with his study of malarial infections. He made several series of temperature readings every three hours in females by inserting hypodermic thermocouples deep into the pectoral muscles. The mean day temperature for all determinations was 42.3°C. ± 0.05, and the mean night temperature 41.0°C. ± 0.26. In certain apparently normal individuals the range might be as much as 6°C. over a 24-hour period. The curves show a sharp drop of temperature beginning about 4:00 P. M., reaching its lowest point about 3:00 A. M. to 4:00 A. M. and then sharply rising.

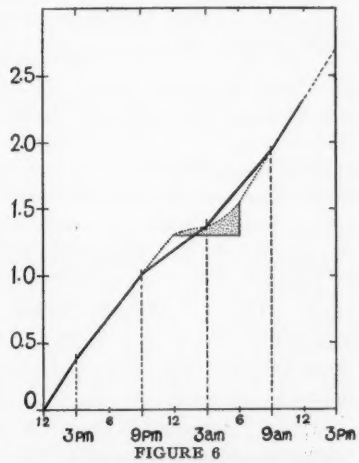


FIGURE 6

Breast feathers. The 9:00 o'clock basis (Fig. 3) modified by the dotted line based on comparison of the 12:00 o'clock basis (Fig. 1) as explained in table 9. The stippled area emphasizes the period of the least six-hour increment. Ordinates = millimeters of growth; abscissae = time of day.

In attempting to compare the diurnal curve of growth with that of internal body temperature in fowl, we are limited by the lack of continuous records of the latter under controlled conditions. Simpson and Galbraith ('05) record almost a plateau of low temperature from 9:00 P. M. to 3:00 A. M. from observations of a single male and female Dorking fowl. In canaries (Huff, '39) the high daytime body temperature begins to fall in the late afternoon and reaches its lowest point about 3:00 A. M. to 4:00 A. M. and then rises sharply. If it is permissible to combine observations on temperature in different species of birds for comparison with our growth rate on fowls we note that the rather sudden rise in body temperature about 3:00 A. M. to 4:00 A. M. agrees well with the sudden increase of rate

of growth of the feather at the same time, and the association of the regularly occurring night depression of body temperature and growth must be held to be significant. Precise comparisons would require simultaneous determinations of body temperature and rate of growth of feathers under carefully controlled conditions.

It would seem to be indicated that daily fatigue followed by rest involves a decrease of the rate of basal metabolism, which causes a drop in body temperature associated with a reduction in rate of growth of the regenerating feather. The fact that day-night body temperature relations are inverted in nocturnal birds would seem to indicate that light as such does not play a direct rôle in the presumed sequence of events.

2. *Morphological Consequences of the Diurnal Rhythm.*—The determination that the rate of growth undergoes a very sharp diminution each 24 hours between midnight and 3:00 A. M. checks well with C. O. Whitman's discovery of the fundamental bars of feathers, which have been especially studied by Riddle ('07, '08). Riddle believed, on the basis of good evidence, that each bar represents a single day of growth, and that the "defective lines, or points of apposition of the fundamental bars," are the loci of formation of the abnormal fault bars, characterized by absence or defect of barbules, which occasionally cross the vane of feathers at a constant angle. The fault bars were subsequently studied by Fraps and Juhn ('36) and interpreted as isochrones, i.e., as lines of simultaneous disturbance of development in the germ, in their entire extent, thus referable to a cause acting at one time.

H. and Josephine Michener ('38) have described bars that occur in flight feathers of house finches also which they studied during regeneration after plucking. They conclude that the bars across the feathers, resembling watermarks in paper, represent a single day's growth. They find that they are most distinct in winter-grown feathers and surmise that they are due to difference in metabolism at night and in the day.

It is indeed probable that the fundamental bars of feathers are related to diurnal physiological rhythms, but this remains at present hypothetical. The occurrence of such considerable depression of the growth rate of developing feathers during the night as we have determined for fowl offers a better mode of attack on this problem; for it has been established that thresholds of reaction in developing feathers vary according to rate of growth (Juhn and Gustavson, '32; Juhn, Faulkner and Gustavson, '31); moreover, Lillie and Juhn ('32, p. 170) have shown that component parts of the same feather, such as barbules and melanophores, have differential thresholds. On such a basis it should be possible to investigate more precisely than has hitherto been done the fundamental bars and other possible morphological consequences of diurnal rhythms in feathers.

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# THE PIGMENT-FORMING POTENCY OF EARLY CHICK BLASTODERMS

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Recent transplantation experiments[2,3,8] between various breeds of fowl have clearly established the origin of melanophores in the chick from the neural crest. According to Holmdahl[4] this structure first appears in the midbrain region at the 6 somite stage. By this time the greater portion of the medullary plate has been converted already into the neural tube and the three primary regions of the brain differentiated. The question comes up as to where the cells with pigment-forming potency are located before there is any definite morphological indication of the neural crest. To answer this the present experiments were undertaken. Small measured pieces, on the average 0.5 mm. square, were isolated from blastoderms varying in development from the unincubated stage to 8 somites, and transplanted to the right wing bud region of 70–80 hr. host embryos of a different breed. For a description of the methods of cutting and handling small pieces of early blastoderms and grafting to the wing bud, the reader is referred to former publications.[6,7,11]

In the majority of cases the donors were Barred Plymouth Rocks and the host White Leghorns, but Black Minorcas and a $F_1$ hybrid black breed (Barred Plymouth Rock ♀ × Rhode Island Red ♂) also served as donors, and New Hampshire Reds and White Wyandottes as hosts.[13]

A total of 185 operated host embryos lived to attain full down plumage and were examined for pigment formation in the feather cells. Of these 74 (40%) actually hatched, the great majority of which lived to be adults and were followed through their various plumage changes.

*The Experiments.*—a. *Donors 1–8 somites.* Transplants from Barred Plymouth Rock donor blastoderms which included portions of the neural tube, brain wall and Hensen's node or regions not more than 0.3 mm. lateral and posterior to it, produced extensive areas of black down feathers on White Leghorn hosts covering the wing (cf. Fig. 2) and often adjacent regions of breast and back. Transplants from all other regions, the primitive streak, somites, lateral and anterior portions of the area pellucida gave negative results, i.e., produced no black color in the down feathers of the White Leghorn hosts. In donors of 6, 7 and 8 somites, no transplants were taken from the midbrain region in order to be sure to exclude neural crest cells which at this time are beginning to proliferate there.

b. *Head-process donors.* To test the capacity of all regions of the blastoderm at various stages of head-process development for pigment pro-

duction, the entire area pellucida was divided by means of transverse and longitudinal cuts into a number of small pieces (Fig. 1) and each transplanted separately to the wing bud of a host embryo. Record was kept of the original position of each piece with reference to the primitive pit, which marks the center of the node region and is a convenient point from which to take measurements. Blastoderms of Barred Plymouth Rock were tested on White Leghorn and New Hampshire Red hosts, Black Minorca on White

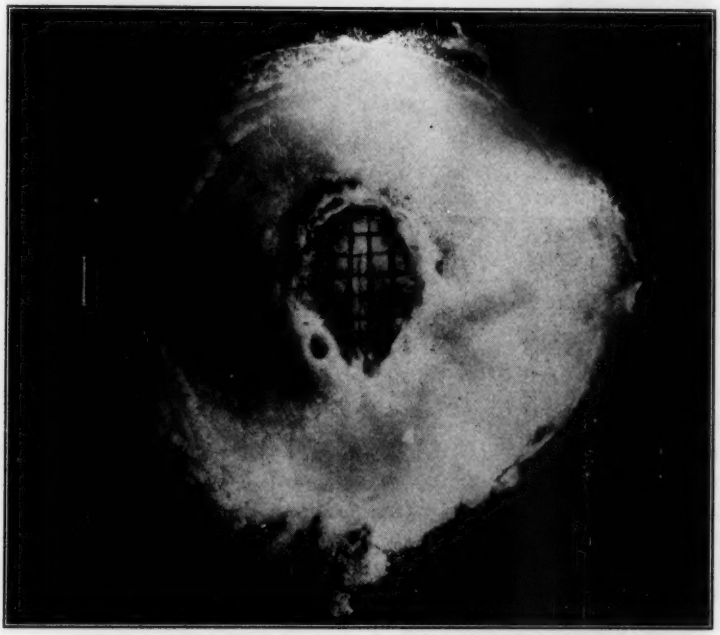

FIGURE 1

Photomicrograph of a living donor blastoderm of the definitive primitive streak stage divided into a number of small measured pieces preparatory to transplantation. See text. (× 10.)

Leghorn and $F_1$ hybrid black on White Leghorn and White Wyandotte hosts.[13] It was soon discovered that pieces from various regions of the blastoderm differed strikingly in their ability to produce pigment in the host. Those which included any part of the head-process, Hensen's node, or a strip 0.3 mm. to each side of them extending from slightly less than 0.1 mm. in front of the process tip to 0.4 mm. behind the primitive pit, produced extensive patches of donor-colored (black) down in the wing and adjacent regions of the Red and the White hosts (Fig. 2). Pieces from all

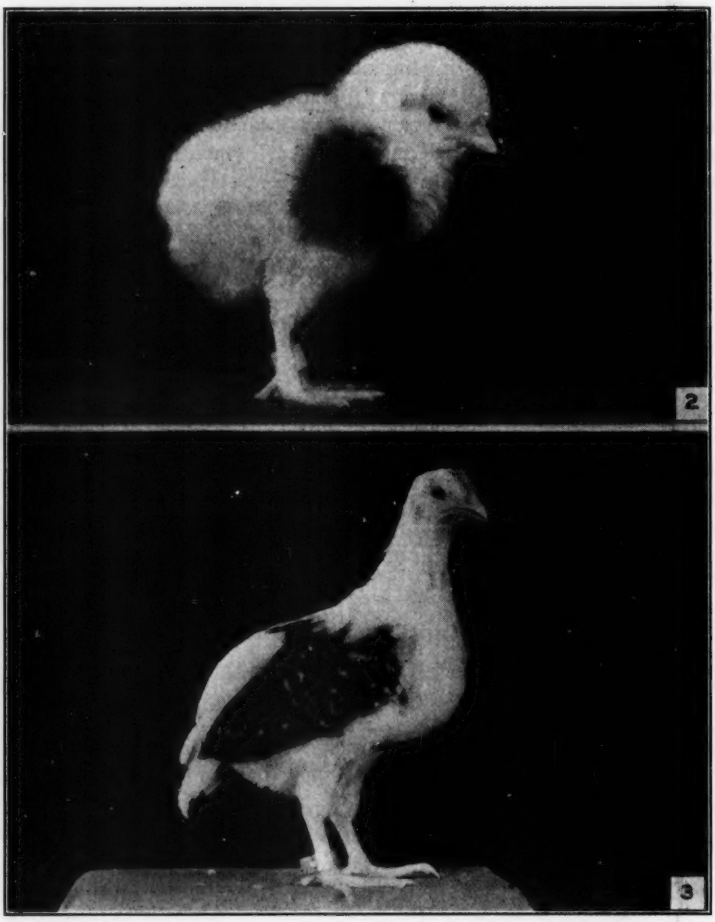


FIGURE 2

White Leghorn chick 3 days after hatching which received in its right wing bud at 75 hours' incubation a transplant including the posterior portion of Hensen's node from a head-process blastoderm (20 hrs.' incubation) of a $F_1$ hybrid black donor. Note the black (donor-colored) down plumage covering the entire wing.

FIGURE 3

White Leghorn pullet 44 days after hatching, whose right wing bud at 79 hours' incubation received a transplant including a part of the posterior portion of Hensen's node from a definitive primitive streak blastoderm (17 hrs.' incubation) of a Barred Plymouth Rock donor. Note the donor Barred pattern of the juvenile wing plumage.

other regions, i.e., posterior half of the primitive streak, anterior and lateral peripheral portions of the area pellucida invariably gave negative results, i.e., produced no pigment.

In all of these experiments the grafted piece often underwent self-differentiation giving a mass of tissue at the base of the host wing. This was true regardless of whether or not a pigmented area resulted and served particularly well to show that failure to give pigment was no sign that the graft had not persisted.

c. *Primitive streak donors.* Blastoderms showing definitive primitive streaks were tested like the head-process blastoderms just described. Figure 1 shows how the area pellucida is divided into a number of small measured pieces by appropriately placed cuts made with a glass needle. As in the preceding series, so here, it was soon clear that transplants from some portions never produced pigment in the host feathers while those from other parts of the same blastoderm regularly gave extensive donor-colored feathered areas (cf. Figs. 2 and 3). Although the region yielding positive results in the primitive streak blastoderm is quite similar to that of the head-process stages in that it is confined to the region of Hensen's node, it is more restricted in its total antero-posterior length due to the absence of the head-process. Pieces taken outside of an area 0.25 mm. lateral, 0.25 mm. anterior and 0.3 mm. posterior to the primitive pit usually do not produce pigment in the host feathers. In one exceptional case a trace of pigment resulted from grafting a posterior piece cut 0.4 mm. from the primitive pit. The best effect is always brought about by pieces actually containing a part of the node itself.

d. *Unincubated or pre-streak donors.* Barred Plymouth Rock and White Leghorn breeds were used exclusively in this series as donors and hosts, respectively. The donor blastoderm was divided as customary into a number of pieces (9 to 16 usually) somewhat larger than in the preceding series. Cuts were made with reference to the antero-posterior axis which was determined by the somewhat variable rule of von Baer (relation of embryonic axis to egg axis). After the blastoderm was removed from the yolk it was carefully examined under a binocular dissecting microscope for any morphological distinction between anterior and posterior ends. The variability in the anterior extent of the endoderm is often the basis for this distinction. No blastoderm was used which showed any visible evidence of primitive streak formation. In only two cases from a total of 34 which lived past feathering were the host feathers pigmented. In both the entire wing was affected. Since the transplanted piece in these two cases was located within the posterior half of the blastoderm, the region concerned in primitive-streak formation, it would appear that here too the area capable of producing pigment is associated with the primitive streak. Until more positive cases are obtained nothing more precise can be said about its

localization. In ten of the negative cases the grafted piece itself differentiated into a small lump of tissue at the wing base.

The experimental results just described show very clearly that early blastoderms can produce pigment in host feathers long before there is any morphological indication of the neural crest (Figs. 2 and 3). The resultant donor-colored areas thus produced are identical in every respect with those obtained by grafting either neural crest or various tissues of the body containing neural crest cells at later periods in development. We know from these earlier experiments that the feathers of the graft area arise from host epidermal cells;[7,12] the transplant furnishes only the melanophores which migrate into the developing host feather germs where they function perfectly normally in their new environment, even to the extent of reproducing the exact donor feather pattern (e.g., barring, Fig. 3). This effect, however, is not lasting. Ultimately the donor-colored area becomes like the host. This change usually occurs during or at the end of the development of the juvenile plumage, so in relatively few cases donor-colored adult feathers appear. In the present experiments with early blastoderms there has been a marked tendency for the color to persist in the adult feathers of the affected area (wing and breast). In one very nice case obtained from grafting the posterior half of Hensen's node (head-process stage) from a Barred Plymouth Rock donor, the White Leghorn host regenerated a complete set of adult feathers with the Barred pattern. When these were replaced after the first molt the region (wing and adjacent breast) became entirely white (host-colored). So the effect was only prolonged a feather generation. This tendency of the donor-color to persist presents a problem of considerable interest. Perhaps more of the melanophore-forming material is carried into the host with pieces from the node region than with pieces of skin ectoderm or mesoderm of similar size from later stages. Further experimentation is of course necessary to validate this.

*The Relationship of the Pigment-Forming and the Neural-Forming Areas.*—It has been pointed out already that the region of the presomite blastoderm which brings about pigmentation in the host feathers after transplantation is localized about Hensen's node. We know from vital staining experiments that the ectoderm of this region is destined to form medullary plate. Perhaps more relevant here for comparison are the data from numerous transplantation experiments in which the neural-forming potency of measured pieces of the blastoderm of early stages was tested on the chorio-allantoic membrane and *in vitro* cultures.

In the definitive primitive streak stages Hunt[5] found that central nervous tissue occurred regularly in chorio-allantoic grafts of transverse strips of blastoderm taken within 0.2 mm. anterior or posterior to the primitive pit, that is to say, pieces including Hensen's node. While ganglia and nerve fibres appeared occasionally a little further posteriorly (0.28 mm.), no

nervous tissue occurred beyond 0.3 mm. This posterior extent was, however, increased to 0.4 mm. by Rudnick's[9] data from *in vitro* experiments. Although at this stage the lateral extent of nervous tissue development has

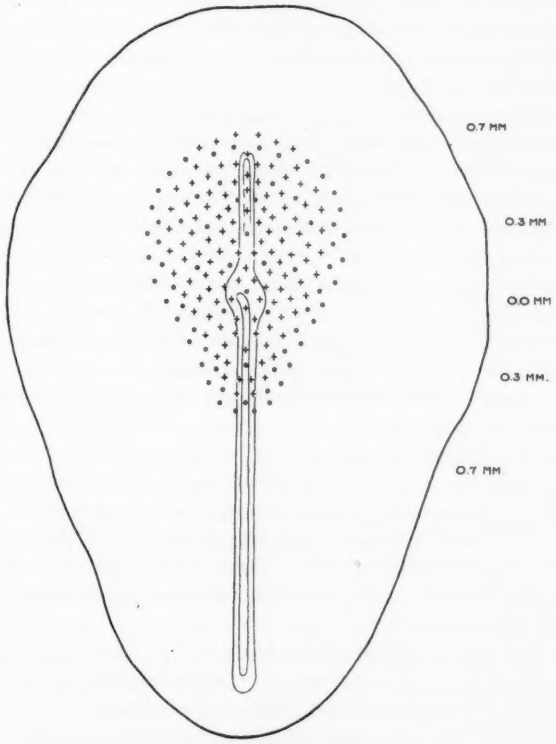


FIGURE 4

Diagram of a chick blastoderm of the head-process stage of development (19–20 hrs.) showing the localization of the area which will produce neural tissue in chorio-allantoic grafts from small measured pieces. (+, brain or neural tube; °, ganglia.) Any part of this same area has the capacity to produce pigment in host feathers.

not been so accurately determined, various data indicate that the neural-forming potency diminishes progressively laterally just as it does anteriorly and posteriorly with increased distance from the primitive pit, falling somewhere between 0.2 and 0.3 mm.

With the development of the head-process (notochord) the antero-posterior extent of the medullary field is increased and the region which will now give nervous tissue in chorio-allantoic grafts is centered about the head-process as well as the node. Figure 4 represents diagrammatically the area from which nervous tissue has developed in chorio-allantoic grafts from small measured pieces taken from blastoderms in the head-process stage.[6] The plus signs indicate central nervous tissue, the circles ganglia. It will be observed that the area capable of developing ganglia is more extensive laterally and posteriorly than that giving brain or spinal cord.

Now if we compare the areas which give rise to pigmented feathers with areas from which nervous tissue developed in chorio-allantoic grafts we see a remarkable agreement in the position and extent of the two in the blastoderm. Any part of this neural-forming area will produce pigment if grafted to a host embryo.

Just as all transplantation experiments point to a progressively diminishing capacity for differentiation of nervous tissue in the lateral and postnodal portions of the medullary field, so here we find a similar tendency for a diminution in the quantity of pigment produced. As already pointed out, the greatest pigmentation effect was produced by transplants including the node itself or some part of it.

Later on, with the appearance of somites and medullary tube, the node region still continues in its parallel rôle of nervous tissue development in chorio-allantoic grafts and of pigment formation in host feathers. In fact even at 33 and 48 hrs.' incubation (approximately 15 and 30 somites) Watterson[10] has obtained extensive areas of black down feathers on White Leghorn hosts from implants of Barred Plymouth Rock blastoderms containing the node or a part of it.

In the pre-streak (unincubated) stages it has been more difficult to establish a direct connection between the neural-forming and the pigment-forming regions in view of the fact that so few positive cases of pigment formation have so far been obtained. Yet, inasmuch as both of the positive cases came from transplants within the posterior half of the blastoderm, the region definitely concerned with primitive streak formation, they do seem significant and, indeed, sufficient to suggest strongly that the same relationship which has been clearly established for all the other stages examined, does exist here, too. There is certainly no reason on the grounds of embryonic development to expect the unincubated (pre-streak) blastoderm to behave differently in this particular respect. Butler's[1] experiments have shown quite clearly that the posterior quadrant of the blastoderm at this stage has the capacity to develop all the axial embryonic structures with a high degree of differentiation, although with lower frequency than older stages. She found that subdividing the posterior half greatly hindered the expression of its developmental capacity. It is

possible that the very small pieces used in the present experiments may have something to do with the preponderance of negative results. Experiments now in progress should settle this point.

*Evidence of a Progressive Change in the Pigment-Forming Area.*—From the foregoing study we have seen that at the definitive primitive streak stage any part of an area approximately 0.6 mm. long × 0.5 mm. wide surrounding and including Hensen's node can, if grafted, produce pigment in host feathers. No other region of the blastoderm has this capacity. A little later when the node begins to regress and leave in its wake the differentiated notochord (head-process) and medullary plate we find that the area capable of producing pigment still centers about Hensen's node (0.3 mm. to each side of the primitive pit and 0.4 mm. posterior) but the anterior extent has increased, depending upon the length of the head-process. So, the region now totipotent for pigment formation includes the tip of the process and a region 0.3 mm. to either side (medullary plate). Thus in a medium head-process stage (Fig. 4) the dimensions of this area are approximately 1 mm. long × 0.6 mm. wide. As development continues anterior to the node with the folding of the medullary plate into a tube and the formation of somites, we find now that any portion of the medullary tube itself will give pigment if grafted but not the adjacent regions as somites, for example. (The node apparently retains its pigment-forming ability as long as it is capable of differentiating nervous tissue.) With the appearance of the neural crest the potency to form pigment becomes restricted to the dorsal half of the neural tube[8] and finally to the neural crest only. Thus we see that in the early periods of development (before the appearance of the neural crest) the potency of the pigment-forming area far exceeds its prospective value. As with other embryonic organ-forming areas such as the eye, heart, kidney, etc., so here, there is a gradual restriction of potency until the formation of a definite primordium. As regards the pigment-forming area, we have seen that in the early developmental stages it coincides with the area which will produce nervous tissue in chorio-allantoic grafts. However, with the appearance of a definite morphological structure—the neural crest—the capacity to form melanin pigment is somehow taken over completely by this particular neural derivative.

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[4] Holmdahl, D. E., *Zeit. mikro-anat. For.*, **14**, 99–298 (1928).
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[8] Ris, H. (in press, 1940).
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[10] Watterson, R. L., *Anat. Rec.*, **72**, Sup. 100–101 (1938).

[11] Willier, B. H., Rawles, Mary E., and Hadorn, E., *Proc. Nat. Acad. Sci.*, **23**, 542–546 (1937).

[12] Willier, B. H., and Rawles, Mary E., *Ibid.*, **24**, 446–452 (1938).

[13] The reciprocal transplantation of White Leghorn to Barred Plymouth Rock and $F_1$ hybrid black hosts gave negative results just as the earlier experiments with head skin ectoderm.[11,12] While transplants from White Leghorn donors not infrequently produce small areas of white feathers on Black and Buff Minorca hosts, such a result is very rare with Barred Plymouth Rock hosts (4 cases, unpublished data). The behavior of the White Leghorn donors in this respect differs from that of White Wyandottes and White Silkies, which regularly give rather extensive white feathered areas when grafted to pigmented hosts (Barred Plymouth Rock, $F_1$ hybrid black, Black Minorca).

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